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Genetic demographic and ecological effects of habitat fragmentation

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GENETIC, DEMOGRAPHIC, AND ECOLOGICAL EFFECTS OF HABITAT FRAGMENTATION

by

David Andrew Tallmon

Presented in partial fulfillment of the requirements

for the degree of

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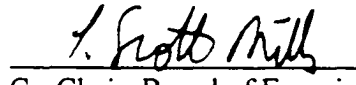

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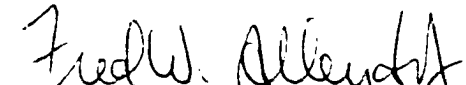

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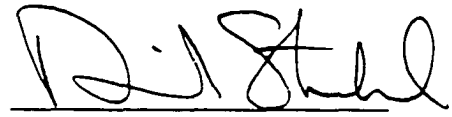

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Tallmon, David A., Ph.D., May 2001 Organismal Biology and Ecology

Genetic, Demographic, and Ecology Effects of Habitat Fragmentation

Co-Directors: Fred W. Allendorf, L. Scott Mills

Habitat fragmentation is a leading cause of the loss of biodiversity. The direct and indirect ecological effects of habitat fragmentation are poorly understood. I used a combination of genetic, demographic, and experimental tools to investigate the effects of habitat fragmentation on the California red-backed voles (*Clethrionomys californicus*) and deer mice (*Peromyscus maniculatus*) in forests of southwestern Oregon.

Demographic and genetic data provided insights into vole population ecology that would not have been possible with only one type of data. Vole abundances fluctuated greatly at sizes below 50 individuals per fragment. I analyzed variation in mtDNA and five nuclear microsatellite loci in vole samples collected from two forest fragments and two unfragmented control sites in 1998 and 1999. Fragments had significantly lower mtDNA allelic diversity than controls, but not nuclear heterozygosity or numbers of alleles. The use of only trapping and mtDNA marker data would imply that fragment populations are at least partially isolated and vulnerable to inbreeding depression. In contrast, the combined abundance estimates and all genetic data show that small fragment populations must be linked to nearby forests by high rates of gene flow, which is probably male-biased. This immigration is likely important to the persistence of small vole populations on forest fragments. However, experimental evidence suggests that the ability of dispersing voles to inoculate seedlings in clearcuts surrounding fragments with ectomycorrhizal fungi, which are essential for forest regeneration, may be limited by abiotic conditions in clearcuts. I found no evidence of reduced fitness (adult survival) on fragments relative to controls.

I found positive effects of fragmentation on deer mice and negative effects of mice on trillium (*Trillium ovatum*), an understory plant that shows reduced recruitment and increased extinction risk in fragmented forests. Multi-strata and closed population mark-recapture models showed that mouse survival was highest in clearcuts, intermediate on forest fragments, and lowest in contiguous forests. Matrix projection models suggested this should result in drastic differences in habitat-specific population growth rates. In agreement with this, mouse densities were higher in fragmented than in unfragmented forest sites. Predation on trillium seeds was higher in areas of higher mouse relative abundance.

These results provide evidence of subtle, yet important population and community level impacts of fragmentation. For California red-backed voles, there was no detectable fitness effects of habitat fragmentation, but their ecological role as ectomycorrhizae dispersers appears to be compromised in clearcuts. There also appears to be mechanism for a human-caused trophic cascade in which positive effects of fragmentation on deer mouse demography lead to increased predation rates and extinction risk for trillium populations.

ACKNOWLEDGEMENTS

There are many people who have contributed to my dissertation. It is not possible to provide due thanks to them here. I want to emphasize that the strengths of this dissertation reflect the work of many, from advisors to field assistants. Any oversights or mistakes it contains are mine.

My co-advisors, Scott Mills and Fred Allendorf, have taught me a great deal about the being a scientist and about life. I am better for my experiences with them and will always draw upon what I have learned. My dissertation committee members, including Len Broberg, Doug Emlen, Kerry Foresman, and Robin Waples, have also been helpful.

There are many lab and field assistants who have put forth admirable efforts to make this dissertation possible. They include Jared Baecker, Hope Draheim, Kevin Fairhurst, Christine Grosse, Gong Ji'en, Kingsford Jones, Nicole Nolte, Jessie Newby, Todd Ondick, Nikki Radke, and Mandy Stone. I am deeply indebted to them. I also thank Kevin Lair and Mike Schwartz for help in the lab. Special efforts from Hope Draheim, Kevin Fairhurst, and Nikki Radke resulted in undergraduate projects that I supervised and that are incorporated into chapters 2, 3, and 5. King Jones provided much of the effort that resulted in the manuscript that composes Appendix 4. I want

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CHAPTER 1 – Introduction

BACKGROUND

Habitat fragmentation is the most serious human-caused threat to biological diversity (Myers 1979, Harris 1984), because it results in the loss of existing habitat and increased isolation of remaining populations. Habitat fragmentation can have a range of direct and indirect impacts on natural communities, ranging from alteration of microhabitats (Chen et al. 1990) to interactions among species and trophic cascades (Crooks and Soulé 1999). The changes that may ensue following habitat fragmentation would not be of great concern if habitat fragmentation were not so widespread. As reported by Laurance (2000), tropical forests are currently being logged at a rate of six million hectares per year, which is an area roughly twice that occupied by Belgium. In the Pacific Northwest, it is estimated that 85% of the old-growth forests that once covered western Washington and Oregon have been logged (Booth 1991). As a result, changes in microhabitats or interactions among species documented on a small-scale may have important ramifications on a regional scale, if extrapolated from the scale at which ecological studies are typically conducted to the vast scale at which habitat fragmentation has occurred.

Obvious impacts that accompany habitat fragmentation include alteration of the physical structure of an ecosystem. This is especially apparent in forested landscapes, where fragmentation translates into the removal of large standing trees -- sometimes all of them. This can result in dramatic impacts in the abiotic and biotic conditions of forests (Harris 1984, Chen et al. 1992). It has been documented that in tropical forests of Brazil

that remaining habitat patches continue to lose biomass, due to tree mortality, several hundred meters from the forest-clearcut edge (Laurance et al. 1997). Consequently, habitat fragmentation can continue to alter the physical structure and quality of remaining habitat long after initial fragmentation has occurred.

The mechanisms by which habitat fragmentation can act can also be subtle. Perhaps the most subtle and often controversial threat facing fragmented populations is the loss of genetic variation and how this affects population dynamics. Theory shows that small populations will lose genetic variation (Wright 1931). The loss of genetic variation in finite populations can lead to a decrease in demographic vital rates (survival and fecundity) that influence overall probability of population persistence (Mills and Smouse 1994). However, convincing empirical evidence to support this theoretical link between genetic variation and population persistence has only recently been collected (Newman and Pilson 1997, Saccheri et al. 1998).

Habitat fragmentation can also have non-genetic impacts that are difficult to document. For example, even in the absence of genetic changes, habitat fragmentation can directly decrease vital rates. In forests of the Pacific Northwest, the commonly cited example of negative demographic effects of habitat fragmentation has been the Northern spotted owl (Franklin et al. 2000), which is thought to suffer reduced survival as a result of industrial forestry.

For a species that is abundant or that strongly interacts with other species, demographic changes can lead to changes in other species in the same or different trophic levels (Power et al. 1996). Consequently, demographic impacts that may or may not be apparent for a single species can translate into cascading effects through the ecological

community (Crooks and Soulé 1999). However, we have few examples to show these relationships across different levels of biological organization and, as a result, little ability to determine when and where they might be coupled.

RESEARCH OBJECTIVES AND FINDINGS

There is little doubt that habitat fragmentation impacts natural populations. The challenge lies in understanding exactly how this occurs. The basic objective of this research was to understand large-scale patterns that result from habitat fragmentation by linking investigations of the genetic, demographic, and community-level impacts of forest fragmentation on small mammals in southwestern Oregon. Only after linking studies at different biological levels can we make fully informed decisions about the cumulative ecological impacts of different human activities at local, regional, and global scales, and begin to predict how human-caused perturbations will affect natural communities.

I focused my investigations upon two small mammal species commonly found in the forests of southwestern Oregon, the California red-backed vole (*Clethrionomys californicus*) and the deer mouse (*Peromyscus maniculatus*). The California red-backed vole has been known for decades to be negatively impacted by clearcutting in Pacific Northwest forests (Tevis 1956, Gashwiler 1959). More recent results, upon which this research builds, point to possible isolation and the loss of genetic variation in vole populations on forest fragments (Mills 1993, 1995). Because studies have suggested that the this vole is also ecologically important (Maser et al. 1978), and because it has useful properties as a model species (*e.g.*, locally abundant, short generation interval, small

home range size), it was a logical target species for investigations of the effects of habitat fragmentation.

I examined the genetic and demographic structure of California red-backed voles in fragmented and unfragmented forests of southwestern Oregon. I also examined how fragmentation might also affect the ecological role of this species as a disperser of the ectomycorrhizal fungi needed by conifers in this region. The specific questions I asked are listed below and I address them in chapters 2, 3, and 4, respectively.

- Has habitat fragmentation led to isolation and a loss of genetic variation in vole populations?
- Has habitat fragmentation led to a loss of fitness in vole populations?
- Can voles effectively disperse ectomycorrhizal fungi into clearcut areas?

The trapping data I collected suggested that vole populations on forest fragments surrounded by clearcuts were small (< 50 adults) and isolated. However, although few voles were trapped in the clearcuts and habitat fragmentation has clearly impacted the distribution of vole across the landscape, the genetic data provided no evidence that these small populations have lost heterozygosity or allelic diversity. By using a combination of genetic and demographic data, I determined that these populations are not isolated, and that gene flow into fragment populations is probably male-biased. In addition, I found no evidence that the fitness of voles, as assayed by measuring adult survival, is lower on fragments than in unfragmented control sites. These results highlight the increased inference gained by combining genetic and demographic data. Experimental work provided no evidence to support the idea that voles dispersing through clearcuts are capable of effectively inoculating seedlings with ectomycorrhizal fungi spores --

implying that the ecological role of voles in fragmented landscapes may be compromised, despite little evidence of demographic and genetic changes in remaining vole populations.

The deer mouse has also long been studied in forests of the Pacific Northwest. Some studies have found a positive effect of clearcutting on deer mouse populations (*e.g.*, Hooven and Black 1976, Tevis 1956, van Horne 1981, Mills 1996), whereas other have found no effect (Petticrew and Sadleir 1974, Sullivan 1979). During the course of my field research I became interested in whether or not clearcutting favored deer mice, and what implications this might have for the understory herb trillium (*Trillium ovatum*), which Jules (1998) suggested was negatively impacted by mice. In chapter 5, I address the questions:

- Does habitat fragmentation increase deer mouse fitness?
- Is trillium seed predation correlated with deer mouse abundance?

The answer to both questions is "yes". It appears that forest fragmentation has led to vastly increased numbers of mice on a landscape scale, and that a contributing factor to this change is elevated adult survival in clearcuts relative to forest fragments and unfragmented forests. Further, it appears that increased fitness of mice in fragmented forests has contributed to the decline of trillium in the same forests. This provides the first example that I am aware of in which indirect effects of humans on a forest plant are mediated via positive effects on a small mammal. Further, because these species co-exist throughout much of the Northwest, these results may obtain throughout the region.

In addition to research on small mammals, I was also involved in other activities that are described in this dissertation. The Appendix contains a manuscript that is the

result of research conducted with Kingsford Jones, a field assistant of mine in 1997 and 1998. This study documents negative effects of forest fragmentation on artificial bird nests, and suggests that increased nest predation along the edges of forest fragments may be due to differences in the composition of the predator community between fragmented and unfragmented sites.

Throughout the course of this research I was supported by a National Science Foundation graduate training grant fellowship. The purpose of this fellowship was to train graduate students for careers as scientists in non-academic jobs. This training required an internship at a non-academic institution and a dissertation chapter focused on some aspect of how biology is integrated into policy. I spent a 9-month internship at Olympic National Park from March through November of 2000. During some of my time there, I investigated the integration of biology and policy surrounding salmon conservation. In chapter 6, I use case studies of salmon in the Pacific Northwest to discuss the integration of biology and policy in recent developments aimed to protect and recover salmon under the Endangered Species Act.

Chapter 2 - Ecological Insights into Fragmented Vole Populations from Combined Genetic and Demographic Data

ABSTRACT

We combined demographic and genetic data to evaluate the effects of habitat fragmentation on the population structure of the California red-backed vole (*Clethrionomys californicus*). We analyzed variation in the mtDNA control region and five nuclear microsatellite loci in small samples collected from two forest fragments and an unfragmented control site in 1990-1991. We intensively sampled the same forest fragments and two different control sites in 1998 and 1999. Vole abundances fluctuated greatly at sizes below 50 individuals per fragment. Fragments had significantly lower mtDNA allelic diversity than controls, but not nuclear heterozygosity or numbers of alleles. The use of only trapping and mtDNA marker data would imply that fragment populations are at least partially isolated and vulnerable to inbreeding depression. In contrast, the abundance estimates and microsatellite data show that small fragment populations must be linked to nearby forests by high rates of migration. Combined, the demographic and genetic data provide a clear picture of how habitat fragmentation has affected vole population biology.

INTRODUCTION

Habitat loss and fragmentation threaten species throughout the world. As a result of habitat fragmentation, some species are limited to a small number of habitat patches separated by a matrix of less suitable habitat. This pattern of fragmented populations is often compared to a metapopulation structure, in which physically isolated populations are linked by migration and local extinctions are counterbalanced by recolonization (Hanski and Gilpin 1991).

The rate of migration among populations, which varies greatly among species and landscapes, is an important determinant of the degree to which the metapopulation concept may be appropriate for any given species (Hanski and Gilpin 1997). For example, there may be no immigration into small populations and each population must be considered demographically and genetically independent (Westermeier et al. 1998). This is a non-equilibrium situation in which the rate of extinction exceeds the rate of migration, with regional extinction as the predicted outcome (Harrison 1991). In other cases, migration rates may be so high that individuals may visit many habitat patches throughout their lifetimes. This has been referred to as a patchy population structure, because multiple habitat patches host a single demographic unit (Harrison 1991). In fragmented landscapes, it is important to assess the degree to which populations on habitat patches are independent or linked by migration in order to understand evolutionary processes more clearly and to plan conservation measures effectively.

Species with limited dispersal capabilities are particularly vulnerable to the negative genetic and demographic impacts of habitat fragmentation. Adverse impacts can include a reduction in local population size, reduced migration, increased population size

fluctuations, and inbreeding depression. After roughly a decade of debates over the relative importance of demographic and genetic factors (e.g., Lande 1988), empirical evidence has shown that each can affect vulnerability to extinction (Groom 1998; Newman and Pilson 1998; Saccheri et al. 1998; Soulé and Mills 1999).

Despite the importance of demographic and genetic changes to fragmented populations, very few studies of recently fragmented populations have integrated rigorous demographic and genetic analyses. When rigorous demographic and genetic approaches are not combined, important questions about population structure are left unanswered and understanding of how well theory meshes with real world examples is not improved. For example, mark-recapture data may fail to detect long-distance dispersal events because such events are often rare and difficult to observe (Koenig et al. 1996). Genetic analyses may be superior for detecting dispersal events, but are usually inadequate for estimating migration among populations because the distribution of genetic variation among populations can be the result of historic or current gene flow (Milligan et al. 1994). However, the combination of these two complementary approaches can be used to eliminate confounded interpretations of the effects of fragmentation on wild populations.

We combined genetic and demographic analyses in our study of the California red-backed vole (*Clethrionomys californicus*), a species that is thought to be very important to the fragmented forest communities where it is found. In the region of our study, California red-backed voles depend upon below-ground fruiting bodies, or truffles, of ectomycorrhizal fungi for 70-80% of their diet (Ure and Maser 1982). In turn, truffle specialists such as this vole and the northern flying squirrel (*Glaucomys sabrinus*) are thought to be the primary dispersers of the ectomycorrhizal fungi spores contained in

truffles (Maser et al. 1978). Conifers require mycorrhizal fungi in order to obtain adequate water and soil nutrients for growth, so the decreased abundance and diversity of ectomycorrhizal fungi in clearcuts may explain why some forests are slow or unable to regenerate (Amaranthus et al. 1994; Clarkson and Mills 1994; Hagerman et al. 1999). Given this interesting web of interactions among these forest ecosystem components, any negative effects of forest fragmentation upon voles may have indirect negative impacts upon the dispersal of mycorrhizal fungi and, ultimately, the regeneration of forests from clearcuts.

Trapping studies conducted over the past 50 years have shown that California red-backed voles disappear following clearcutting and burning of coniferous forests (Tevis 1956; Gashwiler 1970), and that they have much more limited movement patterns than other sympatric rodents (Gashwiler 1959). Mills (1995) extended these findings to show more detailed effects of forest fragmentation on California red-backed voles on forest fragments surrounded by recent clearcuts in southwestern Oregon. He found that the relative abundance of voles decreased from the forest interior toward the forest edge and that voles were nearly absent from 5-35 year old clearcuts. In addition, DNA fingerprints of voles from forest fragments showed higher band-sharing than voles from unfragmented (control) forests (Mills 1993; 1995). These data imply possible isolation and inbreeding effects for vole populations on forest fragments.

During the summers of 1997-99, we revisited 12 of the 13 isolated forest fragments studied by Mills (1995; 1996) in the summers of 1990-1991. However, it became apparent after the 1997 field season that adequate sample sizes for rigorous demographic and genetic analyses could not be obtained by trapping a large number of

sites for only a few nights each field season, because voles avoid unfamiliar traps. Therefore, we intensified our trapping efforts at two of the forest fragments and two controls throughout the summers of 1998 and 1999, which permitted us to use rigorous abundance estimates instead of abundance indices (Thompson et al. 1998).

Our primary objective was to investigate the effects of habitat fragmentation on vole population structure by integrating intensive mark-recapture studies and with analyses of mitochondrial DNA (mtDNA) and nuclear microsatellite loci variation. First, we estimated vole abundances on forest fragment and control sites in 1998 and 1999 and asked whether or not fragment populations are small enough to lose variation due to genetic drift. Next, we analyzed vole tissue samples collected in 1990-91 by Mills (1993) and samples collected in 1998 to determine whether or not genetic variation was lower on fragments compared to controls in both 1990-1991 and 1998. Finally, we combined our demographic and genetic data to determine whether or not the observed distribution of genetic variation is consistent with that expected for populations isolated by fragmentation.

METHODS AND MATERIALS

Site Descriptions and Trapping Protocols

The forest fragment and continuous forest control sites we studied are located in the Sucker Creek drainage of southwest Oregon, USA (Figure 1). These forests are dominated by Douglas-fir (*Pseudostuga menzesii*) trees and have herbaceous understories. The fragment sites F1 and F2 (referred to as E and O in Mills 1995) are 3.0 ha and 3.7 ha in size and were isolated from adjacent forests by clearcutting in 1987 and

1981, respectively. We saturated each fragment with a grid of traps spaced at 15 m intervals. F1 was covered with 122 traps and F2 was covered with 154 traps. We also placed a transect of six traps, with 15 m spacing between traps, 50 m from the forest/clearcut edge in each of the four clearcuts surrounding each fragment.

We used the same grid and peripheral transect configuration to trap voles in control sites located in continuous forest (> 1000 ha in size). Control sites C1 and C2 are located greater than 150 m from the nearest forest/road edge near the southern and northern borders of Oregon Caves National Monument, respectively. Site C3 (referred to as G in Mills 1995), is 0.8 km east of C1, and was not used in 1998 or 1999 because it abuts a forest edge. At C1 and C2, we set 102 traps in a 17 x 6 grid with 15 m spacing between traps. In addition, a transect of six traps with 15 m spacing was set parallel to each edge of the grid and 50 m from the grid.

We trapped all four sites (F1, F2, C1, and C2) from June through August of 1998 and 1999. Our first trapping session at each site was eight consecutive nights, which allowed us to capture many unique individuals. All seven subsequent trapping sessions were four consecutive nights. Each evening of the trapping sessions, we baited small Sherman live traps with oat groats, sunflower seeds, and 1 cm^3 of fresh apple. We also placed polyester batting inside each trap, and placed each trap inside a pint milk container that was lined with batting to increase protection from inclement weather. Each morning we checked and closed all traps to minimize mortality. The four trapping sessions conducted on all sites in the summers of both 1998 and 1999 were separated by 16 days, except the first and second sessions of 1998, which were 20 days apart. This trapping approach, referred to as the robust design (Pollock et al. 1990), allowed us to estimate

vole abundance each trapping session and to estimate survival between trapping sessions. Details of the population dynamics of these populations, including sex, site, and time-specific survivorship estimates, are presented elsewhere (Tallmon et al., in prep).

Demography

We recorded individual capture histories for each vole during each trapping session. This allowed us to estimate vole abundance (N) on F1, F2, C1, and C2 each session using closed capture models in the computer program MARK (White and Burnham 1999). Prior to estimating N's, we developed a set of simple models representing possible patterns in the capture and recapture probabilities. These candidate models were necessarily simple due to small population sizes, but they included different combinations of variation in capture and recapture probability among sites and through time (Appendix 1). N's presented in the results are from the candidate model that best described the data collected for each trapping session, as determined using Akaike's Information Criteria (AIC). AIC is a parsimony-based approach used in mark-recapture studies to quantitatively rank candidate models (White and Burnham 1999).

Genetic Analysis

All voles captured were toe-clipped for individual identification and for genetic analysis. We extracted DNA using a Gentra Puregene kit and then analyzed both mitochondrial and nuclear genetic variation. We used modified Kocher primers (Kocher et al. 1989; Shields and Kocher 1991) L16007 (5'-CCCAAAGCTAAAATTCTAA-3') and H16498 (5'-CCTGAAGTAGGAACCAGATC-3') to amplify the mtDNA control

region of individual voles in polymerase chain reactions (PCR; Appendix 2). The PCR profile included a 94°C denaturing phase for 5 min followed by 35 repetitions of this cycle: 94°C for 1 min, 55°C for 1 min and 72°C for 1.5 min. We then incubated the amplified mtDNA from each individual with five restriction enzymes (*Nla III, Mbo I, Hind III, Rsa I,* and *Hae III*) for 6 hours at 37°C. Restriction fragments were electrophoresed through 2.5% agarose gels, and visualized using ethidium bromide staining. We sized mtDNA fragments by comparing them to a 100 bp standard and estimated the allelic diversity within forest fragments and control sites using REAP version 4.0 (McElroy et al. 1992).

We amplified alleles at five microsatellite loci in PCR reactions with primer sequences developed for congenerics by Ishibashi et al. (1997) or Gockel et al. (1997; Appendix 2). Each 10 ul reaction contained 20-200 ng DNA, which we amplified in a thermocycler for 30 cycles with the following temperature regime: 2 min. at 94°C (1^{st} cycle only), 30 s at 94°C, 30 s at an annealing temperature (Appendix 2), and 60 s at 72°C. We ran PCR products in 7% denaturing polyacrylamide gels in 1X TBE buffer, visualized genotypes using a Hitachi FM-BIO 100 scanner, and determined allele size by comparing PCR product lengths to MapMarkerLOW size standards. We included two sample standards on all gels to ensure consistent genotyping.

We analyzed the microsatellite data using the computer programs F-STAT (Goudet 1995) and Genepop (Raymond and Rousseau 1995). Specfically, we used F-STAT to calculate expected and observed heterozygosities, the mean number of alleles per population, and to test for departures from Hardy-Weinberg (HW) proportions. We

used Genepop to test for gametic disequilibrium between each pair of loci in each population and to estimate gene flow.

We tested for differences in mtDNA allelic diversity, nuclear heterozygosity ($\hat{H}_o$) and numbers of alleles ($\hat{A}$) among the four populations sampled in 1998 using a one-way ANOVA that is robust to unequal variances (Rice and Gaines 1989). We treated individuals as replicates for the mtDNA analysis because mtDNA is inherited as a single locus. For the comparisons of nuclear variation, each locus was treated as a replicate (n = 5) and mean $\hat{H}_o$ and $\hat{A}$ across loci were compared among populations.

In order to compare $\hat{A}$ among samples collected in 1990-1991, we developed a TurboPascal (Borland 1991) bootstrapping program (available from senior author upon request). In each of 100 replicates, the program drew alleles from the C3 sample at sample sizes equal to those collected from F1 (n = 16) and F2 (n = 9) in 1990-1991. We did not use a statistical test to compare variation among populations sampled in 1990-1991 because of limited and unequal sample sizes.

We applied population genetics theory to the demographic data in order to infer the expected rate of drift in fragmented populations. In an isolated, finite population, the initial heterozygosity (H_i) will decrease over t generations to a lower level (H_t), following the equation

$$H_t = (1-1/(2N_e-1))^t H_i,$$

where N_e is the effective population size (Wright 1931). Essentially N_e is an adjusted N that accounts for "non-ideal" conditions that occur in natural populations, such as non-random variability in lifetime reproductive success, unequal sex-ratio, and fluctuating

population size, that reduce N_e below N. N_e usually lies somewhere between 30-50% of N in wild vertebrate populations (Kalinowski and Waples 2001).

We used this relationship between N_e and N, our estimates of vole population sizes on fragments, and the simulation model Easypop (version 1.7.1, Balloux 1999) to calculate expected losses of genetic variation for vole populations, assuming that they are truly isolated. This program simulated genetic drift at 5 loci in a randomly-mating population (N_e = 10 or 20) with equal numbers of males and females and H_i = 1.00. We also included mutation in the simulations at a rate of 10^{-2}/locus/generation, in order to make the program more realistic. The expected heterozygosity was recorded at the 20th and 30th generations in each of 50 replicate simulations. In order to determine whether or not the heterozygosities found on the fragments are consistent with those expected for isolated populations, we compared the distribution of the relative reduction of heterozygosity in the simulated populations to the observed reduction of heterozygosity in fragments relative to controls in 1998.

RESULTS

Population Dynamics

We trapped and marked 368 voles at F1, F2, C1, and C2 in the summers of 1998 and 1999. The abundance estimates (N's) were quite small and extremely precise (Figure 2). The abundance estimates had standard errors of nearly zero because capture and recapture probabilities were high. The capture probabilities for each trapping session ranged from 0.92 to 1.00 and recapture probabilities ranged from 0.87 to 0.98 (Appendix 1).

In each session, there were fewer than 50 voles on each fragment (range = 17.00 – 46.02). Because unweaned individuals were not trappable, these abundances represent only the subadults and adults that could be trapped. All populations fluctuated greatly in size both among trapping sessions and between years, but population sizes were generally larger in 1998 than 1999. The turnover of individuals captured in successive trapping sessions was highly variable, with previously uncaptured voles comprising 10-60% of the total individuals trapped in the second through fourth trapping sessions at each site each summer. Three to six individuals survived at each site from 1998 to 1999. Despite our extensive trapping efforts, we detected only one immigration event, in which a vole captured in a clearcut was later captured on a fragment.

Mitochondrial DNA Analysis

MtDNA variation was lower in vole populations on forest fragments than in the control populations. In 1990-1991, F1 and F2 samples had no mtDNA variation and were fixed for the same allele (Table 1). In contrast, $\hat{h} = 0.34$ (S.E.= 0.09) and three alleles were present at C3.

The pattern of lower mtDNA variation on the fragments relative to the controls was consistent in the larger 1998 samples, even though allelic diversity was generally greater in 1998 than 1990-1991. In 1998 samples of over 20 individuals at all four sites, F1 and F2 had significantly lower mtDNA allelic diversity than C1 and C2 ($p < 0.0001$; Table 1). F1 had three mtDNA alleles, but two were represented by a single copy, and F2 was fixed for the same allele present in 1990-1991. In contrast, C1 and C2 had four and

three alleles each, roughly equal allelic diversities of nearly 0.60, and together contained all five alleles observed in this study.

Microsatellite DNA Analysis

In contrast to the mtDNA results, we found extremely high levels of variation at five nuclear microsatellite loci in all populations (Table 2). Three microsatellite loci showed significant departures from HW proportions due to heterozygote deficits in 1990-1991 and 1998 samples. There are many possible explanations for the departure seen at *CRB-5*, *Cgl-15*, and *Cgl-19*, including natural selection, population subdivision, and null alleles. The observed pattern is most consistent with null alleles as the cause. The primers we used were developed for other species, so mutations in primer locations could have caused allele amplifications to fail. In fact, there were 1-3 different individuals that failed to provide PCR products at each of these 3 loci in the 1998 samples, which suggests the presence of null allele homozygotes at fairly high frequencies. Whatever the cause of the heterozygote deficit at *CRB-5*, *Cgl-15*, and *Cgl-19*, it does not appear to have affected the relative amount of genetic variation in fragment and control samples. However, it led us to compare observed heterozygosity ($\hat{H}_o$), rather than expected heterozygosity ($\hat{H}_e$), among populations. Only one of 40 pairwise tests showed evidence of gametic disequilibrium among loci, which is not greater than that expected by chance alone.

In 1990-1991 samples, $\hat{H}_o$ was generally high, but it was lower on the fragments than the control (Table 2). Similarly, the estimated mean number of alleles per locus ($\hat{A}$)

was lower in fragments than the control. Thus, the trends in $\hat{H}_o$ and $\hat{A}$ are consistent with our expectations for partially isolated populations. However, bootstrapping of the C3 data at sample sizes equal to those collected from F1 and F2 in 1990-1991 indicated that $\hat{A}$ is not lower on fragments. In 100 bootstrap replicates of n = 16 and n = 9, C3 showed $\hat{A}$ = 8.69 (var = 0.002) and $\hat{A}$ = 7.33 (var = 0.002), respectively. These are lower values than were observed in F1 ($\hat{A}$ = 10.0) and F2 ($\hat{A}$ = 8.0) samples.

In 1998 samples, which included over 30 genotypes at all sites, neither $\hat{H}_o$ (p = 0.90) nor $\hat{A}$ (p = 0.57) differed significantly among fragment and control sites (Table 2). In addition, $\hat{H}_o$ and $\hat{A}$ did not decrease in F1 and F2 samples from 1990-91 to 1998. In fact, $\hat{A}$ actually increased from 1990-1991 to 1998 in fragments.

DISCUSSION

Ecological and Molecular Evidence for Isolation

Previous studies suggest the California red-backed vole is susceptible to negative effects of habitat loss and fragmentation (Tevis 1959, Gashwiler 1970), including isolation on forest fragments and possible inbreeding effects (Mills 1995; 1996). We found that vole populations on fragments are quite small and that very few voles are ever captured in clearcuts surrounding forest fragments -- implying that the small fragment populations are isolated, at least during summer trapping sessions. The fragment populations also appear to be true populations, and not simply temporary residences, because some adults were present over several consecutive trapping sessions and most were in breeding condition throughout the summer.

The mtDNA data show that fragment populations have reduced genetic variation. This pattern was consistent in 1990-1991 and in 1998 samples. These data imply the possibility of an inbreeding effect, because mtDNA variation was clearly reduced in both fragment populations in both sampling periods. If we had limited our inferences to trapping and mtDNA data, we would have inferred that fragment populations are at least somewhat isolated. This would have been cause for concern because fitness may be reduced in recently isolated, small populations (Newman and Tallmon 2001).

Ecological and Molecular Evidence for Migration

In contrast to the trapping and mtDNA data, the microsatellite data show that inbreeding effects are not currently a threat to the fragment populations. Although 1990-1991 fragment samples appeared to have lower heterozygosity and numbers of alleles per locus than the control, this pattern resulted from sampling error and not underlying biological causes. In 1998, when sample sizes were roughly equal at all sites, heterozygosities in fragment populations were not different from the controls. In addition, there was no evidence for a loss of alleles in fragment populations through time, which is a more sensitive indicator of a population bottleneck than is the loss of heterozygosity (Allendorf 1986). Instead, the mean number of alleles per locus increased from 1990-1991 to 1998 as sample sizes from the fragments increased. The nuclear genetic data refute the hypothesis that vole populations are isolated on fragments and provide insights into the effects of habitat fragmentation on voles that could not be obtained with trapping and mtDNA data alone.

Although the microsatellite data show that the fragment populations are not isolated, these data are of limited usefulness if not combined with the abundance data. In most studies of molecular genetic variation, results showing little loss of variation within populations and little divergence among populations can be interpreted as the result of either large local effective population sizes or ongoing gene flow. That is, the failure to detect any loss of genetic variation in vole populations on forest fragments could be the result of one of two ecological mechanisms that are confounded in most molecular genetic studies. First, the vole populations may be relatively unaffected by genetic drift because, although isolated, large N_e's maintain pre-fragmentation levels of genetic variation. Alternatively, these fragment populations may be small enough to rapidly lose genetic variation to genetic drift, but they are linked to other populations by sufficiently high levels of ongoing gene flow that pre-fragmentation levels of genetic variation are maintained within fragment populations.

Vole abundances on these fragments varied from 17 to 46 subadults and adults, which translate into extremely small N_e's based on previous findings from a wide variety of taxa (Frankham 1995). Assuming *Ne's* of 10 to 20 individuals, 2-3 vole generations per year (Gashwiler 1977) and isolation of these fragment populations of at least 10 years (based on logging records), we would expect the fragment populations should show reduced levels of heterozygosity relative to the control populations soon after fragmentation. In simulations of an isolated population with $N_e = 20$, an average of 33% (SE 5.7%) of the initial heterozygosity was lost within 20 generations, and the minimum amount of heterozygosity lost in any single iteration was 22%. Assuming that the controls represent pre-fragmentation levels of heterozygosity, the fragments should show

at least 22% less heterozygosity than the controls in the 1998 samples if truly isolated by fragmentation. In contrast, the maximum pairwise difference in expected heterozygosity between any control and fragment is 3%, and the observed heterozygosities on fragments are intermediate to the controls. Therefore, we can safely conclude that the small fragment populations are not isolated and have maintained high levels of heterozygosity due to gene flow.

These results imply that a large proportion of the breeders on fragments each generation must be immigrants, because several immigrants per generation (N_em) are necessary to maintain high levels of genetic variation in small populations (Mills and Allendorf 1996), and because N_e's are quite small on fragments. Estimates of the number of migrants per generation (N_em), based on Wright's island model corrected for a finite number of populations (Waples 1998) and the private alleles method of Barton and Slatkin (1986), are 7.7 and 5.3, respectively. These numbers are a large proportion of the effective number of breeders in fragment populations. However, because recently fragmented populations are likely to violate many of the assumptions of these gene flow estimators (Whitlock and McCauley 1999), it is unwise to interpret these gene flow estimates as anything other than qualitative indications of movement among populations.

The disparate pattern in mtDNA and nuclear genetic data is also interesting. Lower mitochondrial variation within fragment populations, without a similar pattern in the nuclear data, may best be explained in two ways. It is possible that since mtDNA has an effective population size one-fourth that of the nuclear genome (Takahata and Palumbi 1985), it is simply a more sensitive indicator of population bottlenecks in these small, fluctuating populations. Alternatively, if migration is male mediated, immigration would

not counter the effects of genetic drift on mtDNA because the mtDNA alleles of immigrant males would not be incorporated into the local gene pool. Our data do not allow us to test these alternatives, but it is worthwhile to note that male-biased dispersal is observed in many rodent species (Chepko-Sade and Halpin 1987).

Conservation Implications

We detected only a single immigration event in five summers of intensive trapping, which suggests voles must be moving into fragments at other times of the year. Whatever the timing of migration events, the primary community-level implication of our data is that voles may well be capable of dispersing mycorrhizal fungi spores as they move through clearcuts between habitat patches. How effectively these voles disperse the spores of mycorrhizal fungi, which are necessary for forest growth and regeneration, remains an important, unanswered question for the health of forest ecosystems.

Vole abundances are mere tens of individuals on forest fragments and fluctuate greatly. Despite small, volatile sizes, the fragment populations do not show a loss of nuclear variation and do not show any evidence of lower fitness (Tallmon 2001). Our combined genetic and demographic data show that the clearcut matrix surrounding forest fragments is not an impermeable barrier to vole dispersal and that immigration of voles into forest fragment populations must be high. Immigration is likely important not only to avoid inbreeding effects in these small populations, but also to avoid extinction due to chance demographic and environmental events that threaten small populations (Lande 1993). Details about the population structure of California red-backed voles described in

this study could not have been obtained without both rigorous estimates of local population sizes and the use of appropriate nuclear genetic markers.

Table 1: Mitochondrial DNA allele frequencies, number of alleles (A), and allelic diversity ($\hat{h}$) in voles samples from forest fragments (F1, F2) and control sites (C1, C2, C3).

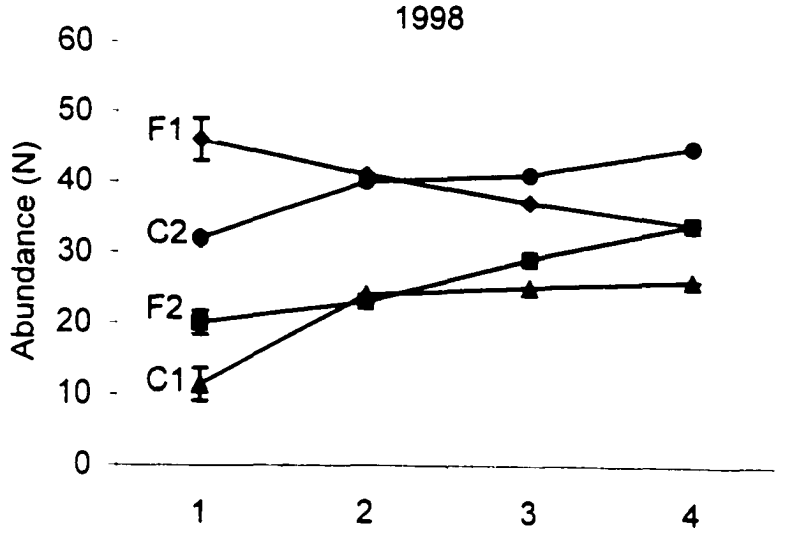
			mtDNA Alleles						
	Site	n	1	2	3	4	5	A	$\hat{h}$ (S.E.)
1990-1991	F1	11	1.00	---	---	---	---	1	0.00 (0.00)
	F2	9	1.00	---	---	---	---	1	0.00 (0.00)
	C3	20	0.80	0.15	---	---	0.05	3	0.34 (0.09)
1998	F1	22	0.91	0.04	0.04	---	---	3	0.17 (0.07)
	F2	21	1.00	---	---	---	---	1	0.00 (0.00)
	C1	23	0.56	0.30	0.04	0.09	---	4	0.59 (0.06)
	C2	22	0.59	0.22	---	---	0.18	3	0.58 (0.08)

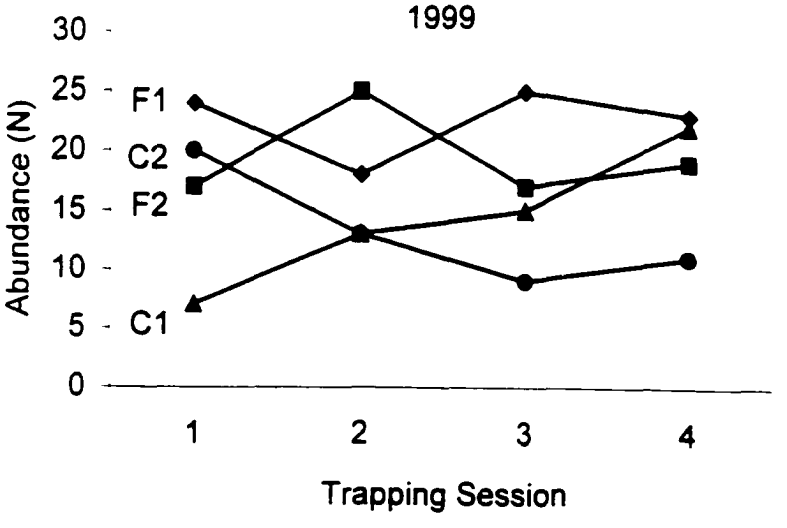
Table 2: The mean number of alleles ($\hat{A}$), observed heterozygosities ($\hat{H}o$), and expected heterozygosities ($\hat{H}e$) at five microsatellite loci in samples (n) from vole populations on forest fragments (F1, F2) and control sites (C1, C2, C3). All statistically significant departures from Hardy-Weinberg proportions were due to heterozygote deficits and are noted by *.

				Locus					
	Site	n		*CRB-5*	*CRB-6*	*Cgl-4*	*Cgl-15*	*Cgl-19*	Mean (SE)
1990-1991	F1	16	$\hat{A}$	12	11	12	6	9	10.0 (2.6)
			$\hat{H}o$	0.67	0.80	0.94	0.46	0.44	0.66 (0.22)
			$\hat{H}e$	0.94*	0.92	0.92	0.76*	0.86*	0.88 (0.07)
	F2	9	$\hat{A}$	9	8	7	7	9	8.0 (1.0)
			$\hat{H}o$	0.40	0.77	0.64	0.64	0.76	0.64 (0.15)
			$\hat{H}e$	0.92*	0.88	0.89	0.87	0.88	0.89 (0.02)
	C3	24	$\hat{A}$	13	12	13	7	10	11.0 (2.6)
			$\hat{H}o$	0.87	0.78	0.91	0.65	0.67	0.78 (0.12)
			$\hat{H}e$	0.91	0.84	0.91	0.83	0.88*	0.87 (0.04)
1998	F1	34	$\hat{A}$	13	10	14	8	11	11.2 (2.4)
			$\hat{H}o$	0.60	0.82	0.88	0.74	0.63	0.73 (0.20)
			$\hat{H}e$	0.91*	0.86	0.91	0.78	0.88*	0.87 (0.05)
	F2	35	$\hat{A}$	13	11	11	9	10	10.8 (1.5)
			$\hat{H}o$	0.81	0.85	0.98	0.48	0.73	0.77 (0.18)
			$\hat{H}e$	0.91	0.87	0.91	0.71*	0.86*	0.85 (0.08)
	C1	36	$\hat{A}$	14	11	14	10	13	12.4 (1.8)
			$\hat{H}o$	0.79	0.71	0.98	0.64	0.48	0.72 (0.18)
			$\hat{H}e$	0.89	0.86	0.91	0.81*	0.91*	0.88 (0.04)
	C2	34	$\hat{A}$	11	11	15	10	11	11.6 (2.0)
			$\hat{H}o$	0.81	0.91	0.77	0.86	0.57	0.78 (0.13)
			$\hat{H}e$	0.89	0.88	0.89	0.83	0.88*	0.87 (0.02)

Figure 1: Map of the area used to study California red-backed vole genetics and demography in fragmented (F1 and F2) and large, unfragmented forests (C1 and C2).

Figure 2: Vole abundances on forest fragment (F1, F2) and control sites (C1, C2) estimated each of four trapping sessions during the summers of 1998 and 1999. Standard errors (SE) are shown only for 1st trapping session of 1998 because high capture and recapture probabilities resulted in SE's of zero in all other sessions.





Chapter 3 - Edge effects, Survival, and Dispersal Behavior of Voles in a Fragmented Landscape

ABSTRACT

We examined demographic and behavioral responses of the California red-backed voles (*Clethrionomys californicus*) to forest fragmentation in southwestern Oregon. Voles were rarely caught in clearcuts, but they did not show a negative response to forest edges on 12 forest fragments surrounded by clearcuts. The first result agrees with a previous study at these study sites, but the latter result does not. Intensive mark-recapture study at a subset of these sites suggested that capture probabilities vary greatly across space and time on these fragments, which may explain the temporal differences in response to edge. The survival of adult voles was not reduced on two forest fragments relative to unfragmented (control) forests. We investigated the dispersal behavior of voles across four clearcut-forest edge interfaces and found no evidence that voles detect and alter their dispersal behavior near forest edges. These results suggest that vole dispersal through clearcuts may be undirected and provide the opportunity for voles to inoculate clearcuts with ectomycorrhizal fungi important to seedlings.

INTRODUCTION

Timber harvest in the Pacific Northwest, USA, has reduced the amount of old-growth forest to roughly 15% of historic levels (Booth 1991). Much of the remaining old-growth has been fragmented into patches of forest with edges adjacent to regenerating clearcuts. This has led to changes in the physical conditions and the composition of these remaining forests (Chen et al. 1992). Consequently, important questions surround the effects of changes in the structure, composition, and abiotic conditions of remaining fragmented forests on resident taxa that evolved in large, intact old-growth forests.

A species that has long been thought to be closely tied to late-succession forests and to avoid clearcut areas is the California red-backed vole (*Clethrionmys californicus*). Studies conducted over the past half-century have shown that red-backed voles are associated with old-growth forest, but absent or rare in forests that have been clearcut and burned (Tevis 1956, Gashwiler 1959). More recently, Mills (1995) found that the relative abundance of voles decreased from the interior toward the edge of forest fragments and that voles were extremely rare in the clearcuts surrounding forest fragments. Further, Mills (1993, 1995) found preliminary evidence of inbreeding effects in a small sample of voles from several differerent forest fragments -- voles from forest fragments showed higher DNA fingerprint band-sharing than voles from contiguous forests. Taken together, the absence of voles from clearcuts and genetic data implied that vole populations on forest fragments may be isolated and possibly vulnerable to inbreeding depression.

These findings are alarming not only for their implications for California red-backed vole population biology, but also in terms of their implications for Pacific Northwest forest community ecology. Coniferous trees of this region depend upon mycorrhizal fungi to obtain adequate water and nutrients for growth and reproduction (Perry et al. 1989). Previous studies have shown that the fruiting bodies of ectomycorrhizal fungi (truffles) are rare in clearcuts (Clarkson and Mills 1994, Amaranthus et al. 1994) and that the diversity and abundance of ectomycorrhizal fungi decreases with increasing distance from forests into adjacent clearcuts (Hagerman et al. 1999, Durall et al. 1999). The red-backed voles' primary food is truffles, and voles are thought to be one of the primary dispersers of the spores contained in these fruiting bodies (Maser et al. 1978). Consequently, the absence of voles from clearcuts may slow the inoculation of clearcut soils with mycorrhizal fungi, which could slow forest regeneration, and the absence of mycorrhizal fungi from clearcuts may slow the re-establishment of vole populations.

The evidence for negative effects of forest fragmentation on vole population dynamics and the implications of these effects for forest regeneration motivated this study of how forest fragmentation impacts the abundance, fitness, and dispersal behavior of red-backed voles in southwest Oregon. First, we repeated the study of edge-effects on the relative abundance of voles at the same forest fragment sites used by Mills (1995) to see if trends he found – decreasing vole abundance along forest edges and isolation on forest fragments – were stable over time. In addition, we intensively studied a subset of these sites to estimate vole abundances on fragments and to determine whether or not survival of adult voles is reduced on forest fragments relative to unfragmented control

sites. Population growth rate in voles is affected more greatly by changes in adult survival than any other demographic rate (Lair and Mills, in prep), so this life history stage provides insight into the fitness consequences of fragmentation on voles. Finally, we investigated the dispersal behavior of red-backed voles in clearcuts to determine whether or not they might be effective dispersers of ectomycorrhizal fungi spores.

METHODS AND MATERIALS

Site Descriptions and Trapping Protocols

Voles were trapped on 11 forest fragments and 2 unfragmented control sites in southwest Oregon, USA (Figure 1). These sites were used previously by Mills (1995) and were all unlogged, late-successional forests, with overstories dominated primarily by Douglas-fir (*Pseudostuga menzesii*) trees and understories of herbaceous plants. However, the fragment sites varied in physical characteristics, including size, slope, aspect, and time since isolation from surrounding forest by clearcuts (Table 1). During each trapping session, each fragment was covered with a grid of Sherman traps spaced at 15 m intervals. In 1997 and 1998, each of the fragments was also surrounded with four transects of 5-6 traps each. We obtained individual capture histories of each vole caught in the four consecutive nights of trapping at each site, using Sherman live traps baited with apple, oat groats and sunflower seeds.

In order to examine the effects of fragmentation on vole survival and absolute abundance, we intensively trapped two of the fragment sites (F1 and F2; named E and O in Mills 1995) and two control sites (C1 and C2), located in continuous forest (> 1000 ha in size) near the southern and northern borders of Oregon Caves National Monument,

respectively. On the control sites, we used the same grid and peripheral transect configuration used on fragments. Specifically, we set 102 traps in a 17 x 6 grid with 15 m spacing between traps at each control site. In addition, a transect of 6 traps with 15 m spacing was set parallel to each edge of the grid and 50 m from the grid.

We trapped these four sites from June through August of 1998 and 1999. Our first trapping session at each site was eight consecutive nights, which allowed us to capture many unique individuals. All seven subsequent trapping sessions were four consecutive nights. Each evening of the trapping sessions, we baited small Sherman live traps with oat groats, sunflower seeds, and 1 cm^3 of fresh apple and fresh polyester batting. We then placed each trap inside a pint milk container that was lined with batting to increase protection from inclement weather. Each morning we checked and closed all traps to minimize mortality. The four trapping sessions conducted on all sites in the summers of both 1998 and 1999 were separated by 16 days, except the first and second sessions of 1998, which were 20 days apart. This trapping design, referred to as the robust design (Pollock et al. 1990), includes secondary periods (each night of trapping) clustered into primary periods (consecutive secondary periods). With this approach, abundances can be estimated each primary period based on secondary period data and apparent survival can be estimated between primary periods (Pollock et al. 1990).

Edge Effects

The vole trapping data were analyzed using a different approach for the two different spatial scales of our trapping efforts: across all 11 fragments versus the two fragments and two controls trapped intensively. We conducted our large-scale analysis of

all 11 fragments following Mills (1995) in order to make our results directly comparable to his findings. The distance from each trap to the nearest forest-clearcut edge was measured and each trap was assigned to one of four edge classes as a function of distance from the edge: 1 (0-15 m), 2 (16-30 m), 3 (31-45 m), or 4 (> 45 m). The relative abundances of voles in each edge class were compared by combining data across forest fragments. At each site, the number of different animals captured in each edge class was weighted by the number of traps in that edge class. At sites for which greater than 1 year of data were collected, values for each edge class were averaged across years. Then, values were averaged across sites to estimate vole abundance as a function of edge class. The relative abundances of voles in each edge classes were compared using a one-way ANOVA that is robust to unequal variances (Rice and Gaines 1989). We also compared the relative abundances of voles in the clearcuts to the fragments using a Behrens-Fisher t-test.

Survival and Abundance

All individuals captured on the two fragments and two control sites that we trapped intensively were assigned to one of eight unique groups. Each group was composed of all individuals of one sex at a site. These data were analyzed using the computer programs RDSURVIV (Kendall et al. 1997) and MARK (White and Burnham 1997). To do this analysis, we first developed a set of models representing possible patterns in the capture, recapture, and survival probabilities (Table 2). We then used RDSURVIV to test for violations of the assumptions of mark-recapture models; homogeneity in capture probability of individuals and independence of individual fates.

We did not find any evidence of violations of the assumptions of mark-recapture theory under the most complicated (global) model, so we compared a set of additional candidate models with different combinations of temporal, spatial, and sex-specific variation in apparent survival (Φ), capture probability (p), and recapture probability (c). The first 15 candidate models were developed before any analysis was conducted and were based on what we thought were reasonable approximations of the dynamics of the study populations (Table 2). Temporary emigration was set to zero in all models because it was not observed frequently enough to be effectively modeled, and we wanted to minimize the number of parameters in these models. Abundances of each sex at each site were also estimated.

All candidate models were run with MARK using a modified step-down approach (see Lebreton et al. 1992, p. 84). We first ran the full (global) model, in which the parameters Φ, c, and p varied among groups independently through time (subscripted $g*t$). Next, we compared this model to others in which the p was constrained, while Φ and c remained general (i.e., $g*t$). After finding the optimal parameterization of p, we stepped through models in which c was constrained. After determining the best parameterization of both p and c, we ran models with these optimized p and c structures and constrained Φ. After the first 15 models were run, we ran three additional models with different constraints on p and c to ensure that we had not mistakenly settled upon suboptimal models.

The best approximating model was determined using Akaike's Information Criteria (AIC). AIC is a parsimony-based approach used in mark-recapture studies to quantitatively rank candidate models (White and Burnham 1999). The model with the

lowest AIC value is the candidate model that most adequately describes the variation in the underlying population dynamics, without including so many parameters such that the precision of parameter estimates is sacrificed.

Movement

We investigated the movement of voles along four clearcut-forest edges using an experimental approach (Zollner and Lima 1997, Gillis and Nams 1998). Voles were trapped in large continuous forest patches away from our study sites. All male and non-lactating female voles > 15 g were kept in small cages for at least 24 hr and then introduced into one of four clearcut-forest sites located > 2 km from the capture location. A clearcut-forest site was defined as one with at least 120 m of linear forest-clearcut edge.

At each site, three release locations were established at 30 m intervals along the edge: 15 m into the forest from the edge, 15 m into the clearcut from the edge, and 30 m into the clearcut from the edge. All releases were made at locations > 90 m from the nearest "non-target" edge between 15 and 30 minutes before dark. At each release site, a randomly selected vole was dipped in flourescent powder (Radiant Color Division, Richmond, CA) and placed in a trap. The trap was then immediately placed on the ground, facing perpendicular to the forest edge, and cracked open.

The flourescent trail left by each vole was identified with a black light the evening following release. A randomly selected point between 3 and 4 m along the trail from the release site was used to begin quantifying movement. This point and all consecutive points at 1 m intervals along the trail (up to 45 m) were then used to measure tortuosity,

correlation, bias, and habitat type (Turchin 1998). Displacement was defined as the linear distance between 1 m intervals along a trail (0 = minimum; 1 = maximum). The correlation among consecutive points along a trail, which also provides insight into the directedness of movement, was determined from the cosine of the difference in compass direction (radians) between consecutive 1 m points (Turchin 1997). Bias is simply the cosine of the difference between the orientation of movement along the trail at a point and the direction toward a putative source of attraction or repulsion at that same point. In this case, the putative source of attraction/repulsion was the forest edge. Thus, bias indicated how strong was the tendency to move toward the edge in the clearcut and how strong was the tendency to move away from it in the forest. Finally, we calculated the mean of each voles' movement characteristics in each of five edge categories: 31-45 m into the clearcut, 16-30 m into the clearcut, 0-15 m into the clearcut, 0-15 m into the forest, and 16-30 m into the forest.

RESULTS

Demographic Responses to Fragmentation

We captured 449 voles at all sites during the summers of 1997-1999. Of these, only 10 voles were captured in the clearcuts surrounding the 12 forest fragments. We detected only one immigration event from a clearcut into a fragment, despite our extensive and intensive trapping efforts. The relative abundance of voles was much lower in clearcuts than in fragments ($p = 0.02$; Figure 2).

Our data provide no evidence of a negative edge effect on the relative abundance of California red-backed voles on forest fragments. Voles did not decrease in relative abundance moving from the interior to the edge of forest fragments ($p = 0.99$).

Estimates of vole abundance and survival in the intensively studied fragments and controls provided further insight into the effects of habitat fragmentation on voles. The top-ranked candidate models all incorporated extensive variation in capture and recapture probabilities, whereas simpler models that constrained these parameters to be similar through time and/or among groups described underlying population dynamics much more poorly. In the top approximating model, the estimates of daily capture probabilities varied from a low of 0.02 (SE = 0.016) at the beginning of the first primary period to a high of 0.82 (SE = 0.032) at the end of the primary periods. Daily recapture probabilities varied across sexes, sites, and through time from 0.04 (SE = 0.036) to 0.92 (SE = 0.080). This variation in capture and recapture probabilities is also reflected in the poor fit (high ΔAIC values) to the data set of simpler models that constrained capture and recapture probabilities to be constant across space and time (Table 2).

There was evidence of extensive temporal and spatial variation in survival. We included several different types of constraints on survival in our models to assess whether or not demographic differences existed between controls and fragments. The best approximating model incorporated unique survival estimates for each group (each sex at a site = a group) that changed between sampling intervals (Φ_{g*t}). Survival varied greatly among these groups across sampling intervals and within groups across primary periods from 0.18 (SE = 0.097) to 1.00 (SE = 0.000) (Figure 3). However, there were no consistent differences in survival between controls and fragments, and models

constrained to differences in survival between fragments and controls received little support (Table 2). There appeared to be some correlation in survival estimates among groups in some of the time intervals, especially in 1999.

Our intensive trapping efforts provided precise estimates of vole abundances. In fact, the standard errors around the population size estimates for each trapping session were not distinguishable from zero, except for two occassions in 1998 on C2 (Table 3). Population sizes on the fragments were small and highly variable, remaining below 45 individuals at each site in all primary periods. There were strong deviations from an equal sex ratio both within sites through time and across sites at each trapping session.

Movement

There was no trend toward increased displacement, bias, or correlation in vole movements closer to the edge (Figure 4). The displacement and the correlation among successive moves were not greater in the 15 m forest or 15 m clearcut edge classes than in the 30 m clearcut edge class. In fact, there was a weak trend in the data toward decreased displacement and correlation among moves in the clearcuts closest to the edge. Furthermore, vole movements were not more biased, or directed toward the edge, at distances closer to the edge than at distances farther from the edge.

DISCUSSION

We found that California red-backed voles were rarely captured in clearcuts surrounding forest fragments, but that there were no negative edge effects on the fragments themselves. The first finding corresponds closely with what Mills (1995) found in the same clearcuts several years earlier. In fact, the capture rates of voles in clearcuts in this study and Mills (1995) are very similar, at 0.003 voles/trap and 0.002 voles/trap, respectively.

The lack of a negative edge effect on the fragments is surprising, because Mills (1995) found a negative edge effect at the same sites several years earlier. We can only speculate on the reasons for the change in patterns over time. It is possible that the vole edge response changed with succession patterns, but this seems unlikely since these sites represent a range of ages since isolation and the two studies were separated by fewer than 10 years. However, because Mills (1995) used an abundance index, and for comparison purposes we repeated the same approach for the large-scale portion of our study, we cannot eliminate the confounding explanation that detection (capture and recapture) probabilities changed over time.

In fact, our analysis of the intensively sampled sites using a statistically based mark-recapture framework, indicates strong spatial and temporal variation in capture and recapture probabilities. Ultimately, the limitations of an relative abundance index-based approach (Nichols and Pollock 1983) prevent us from making strong conclusions about whether abundances or detection probabilities changed over time.

On the intensively studied sites where we investigated survival and abundance using mark-recapture techniques, there was no evidence of reduced vole survival on forest fragments relative to unfragmented sites. The best supported model showed considerable variation in survival by site, sex, and time, and the survival estimates suggest some correlation in the survival of voles at these sites over time. The strong fluctuations in survival imply an important role for demographic stochasticity in these populations. Survival estimates changed greatly between capture periods, which implies that chance events could have profound effects on the persistence of these populations. The correlation in survival between different sexes at different sites implies that environmental variation may also influence vital rates at the scale we examined. However, we do not have any data to suggest which environmental variables may have caused the observed synchrony in adult survival across groups.

In addition to the very low vole numbers in clearcuts, perhaps the most alarming aspect of the demographic data is the small vole population sizes on the forest fragments. Population sizes on the fragments were precisely estimated and were always below 45 individuals in the summers of 1998 and 1999, when vole abundances at these sites should have been near their annual peak. Although these estimates do not include juveniles that were too small to be captured in our traps, it is apparent that few breeders were present on forest fragments at any one time. Furthermore, the population sizes fluctuated greatly between trapping sessions at each site, to as few as 18 individuals at one site. The strong flucuations in adult survival and population sizes mirror one another and suggest that demographic and environmental stochasticity may play a large role in the dynamics of vole populations on forest fragments.

Interestingly, despite small fragment population sizes and little evidence of vole movement through clearcuts surrounding fragment populations, we found no evidence of a loss of genetic variation in fragment populations in a companion study (Tallmon et al., *submitted*). Either dispersers do not enter traps in clearcuts, or dispersal occurs during times of the year when we did not trap. It is likely that the migration we detected with genetic data, but were unable to detect with trapping data, plays an important role in the persistence of these small fragment populations. Clearly, these vole populations are subject to wide fluctuations in adult survival and abundance, so immigration may be an critical force in maintaining these populations through time.

The movement data suggest that voles do not disperse toward forest fragment edges from the clearcut, even at distances of less than 15 m. Although there was considerable overlap in SE values among all edge classes, there were weak trends that suggested voles are less directed in their movements as they approach edges. Either California red-backed voles are unable to visually detect forest/clearcut edges at close distances or are not attracted to them, even within 15 m of the edge. These results contrast with those for the related southern red-backed vole (*Clethrionomys gapperi*) at a grassland/woodland site, which were found to orient toward the woodland at diatances of 15 m or less (Gillis and Nams 1998). However, Zollner and Lima (1997) found no evidence of orientation toward forests at close distance for white-footed mice (*Peromycus leucopus*).

An implication of these results is that California red-backed voles may simply disperse through foreign clearcuts in a random pattern until suitable habitat is encountered. Hayes (1996) suggested that California red-backed voles may be dispersers

of mycorrhizal fungi into clearcuts from adjacent forests. We suggest that the undirected vole movement patterns in clearcuts recorded here would favor the dispersal of mycorrhizal fungi spores in clearcuts, because the rate of vole movement through clearcuts to nearby forests would be relatively slow. Consequently, dispersing voles may be important dispersal vectors for mycorrhizal fungi spores.

We did not detect any negative effects of forest fragmentation on vole fitness or abundance. This pattern was consistent both at the broad and the small geographic scales at which we examined their responses to fragmentation. It appears that vole populations persist on forest fragments as a result of immigration. However, these results do not imply that voles are unaffected by fragmentation – they are rarely caught in clearcuts, so their distribution appears to be limited to remaining patches of forest in a heavily logged landscape. But, it does appear that voles do not respond as strongly to forest fragmentation as was previously thought.

Table 1: Description of forest fragment and control sites used in study of California red-backed vole responses to habitat fragmentation.

Site	Size (ha)	Distance to Forest (m)	Aspect	Slope	Elevation (m)	Year of Isolation	Year(s) Trapped
Fragments							
F2	3.7	150	W	24	1403	1980	'97-'99
F1	3.0	100	W	32	1342	1987	'97-'99
FB	2.0	120	W	25	671	1973	'97, '99
W	1.4	60	SE	14	732	1983	'97, '99
S	1.3	150	E	33	991	1977	'97, '99
YB	1.3	75	N	35	915	1989	'97, '99
HD	1.1	110	S	22	976	1965	'97, '99
Z	1.0	60	S	22	732	1983	'97, '99
PC	0.9	170	N	35	640	1986	'97, '99
JT	0.6	50	E	2	991	1988	'97, '99
F3	0.5	100	W	10	1220	1978	'97-'99
Controls							
C1	N/A	N/A	SW	12	1580	N/A	'98, '99
C2	N/A	N/A	W	25	1510	N/A	'98, '99

Table 2: Description, number of parameters (# P), and performance of candidate models used to examine the effects of forest fragmentation on California red-backed vole adult survival and abundance. Each model contains a different combination of variation in apparent survival (Φ), capture probability (p), and recapture probability (c). The performance of each model, listed in the order run in MARK (Burnham and Anderson 1997), was determined by adjusted Akaike's Information Criteria (ΔAICc).

	Model					
	Φ	p	c	Model Description	# P	ΔAICc
1	g*t	g*t	g*t	global model - Φ, p, c vary independently among groups through time	632	350.88
2	g*t	2°	g*t	p varies same way within trap sessions for all groups; Φ, c vary by group and time	352	200.93
3	g*t	s*1°	g*t	p varies by site and trap session; Φ, c vary by group and time	376	228.36
4	g*t	s	g*t	p site specific; Φ, c vary by group and time	348	481.11
5	g*t	.	g*t	p same among all groups and trap sessions; Φ, c vary by group and time	345	483.34
6	g*t	2°	2°	p, c vary the same within all trap sessions for all groups; Φ varies by group and time	135	162.26
7	g*t	2°	g*1°	c vaires by group and 1° session; Φ varies by group and time; p varies the same within all trap sessions for all groups	192	0.00
8	g*t	2°	s*1°	c unique for each site, each trap session, but constant within each trap session; p varies the same within all trap sessions for all groups; Φ varies by group and time	160	39.94
9	g*t	2°	s	c unique at all sites; p varies the same within all trap sessions for all groups; Φ varies by group and time	132	169.78
10	g*t	2°	.	c constant; p varies the same within all trap sessions for all groups; Φ varies by group and time	129	165.03

	Model					
	Φ	p	c	Model Description	# P	ΔAICc
11	g	2°	g*1°	Φ unique among groups; p varies the same within all trap sessions for all groups; c varies by group and 1° session	144	396.51
12	s	2°	g*1°	Φ unique among sites; p varies the same within all trap sessions for all groups; c varies by group and 1° session	140	390.59
13	c v. f	2°	g*1°	Φ different between controls and fragments, constant through time; p varies the same within all trap sessions for all groups; c varies by group and 1° session	138	387.90
14	s*yr	2°	g*1°	Φ varies independently among sites each year; p varies the same within all trap sessions for all groups; c varies by group and 1° session	144	365.91
15	m v f	2°	g*1°	Φ varies between males and females, but constant through time; p varies the same within all trap sessions for all groups; c varies by group and 1° session	138	390.59
16	g*t	s*1°	g*1°	Φ varies by group and time; p varies by site and 1° session; c varies by group and 1° session	210	443.76
17	g*t	g*t	g*1°	Φ, p vary by group and time; c varies by group and 1° session	256	590.34
18	g*t	2°	s*1°	Φ varies by group and time; p varies the same within all trap sessions for all groups; c varies by site and 1° session	160	39.92

Table 3: The estimated number of voles of each sex (♂, ♀) and total population sizes (bold print) on forest fragments F1 and F2 and control sites C1 and C2 in each of 4 trapping sessions the summers of 1998 and 1999. In most cases, capture probabilities were so high within primary trapping sessions that abundance estimates had extremely high precision. SE's are shown only where > 0.01.

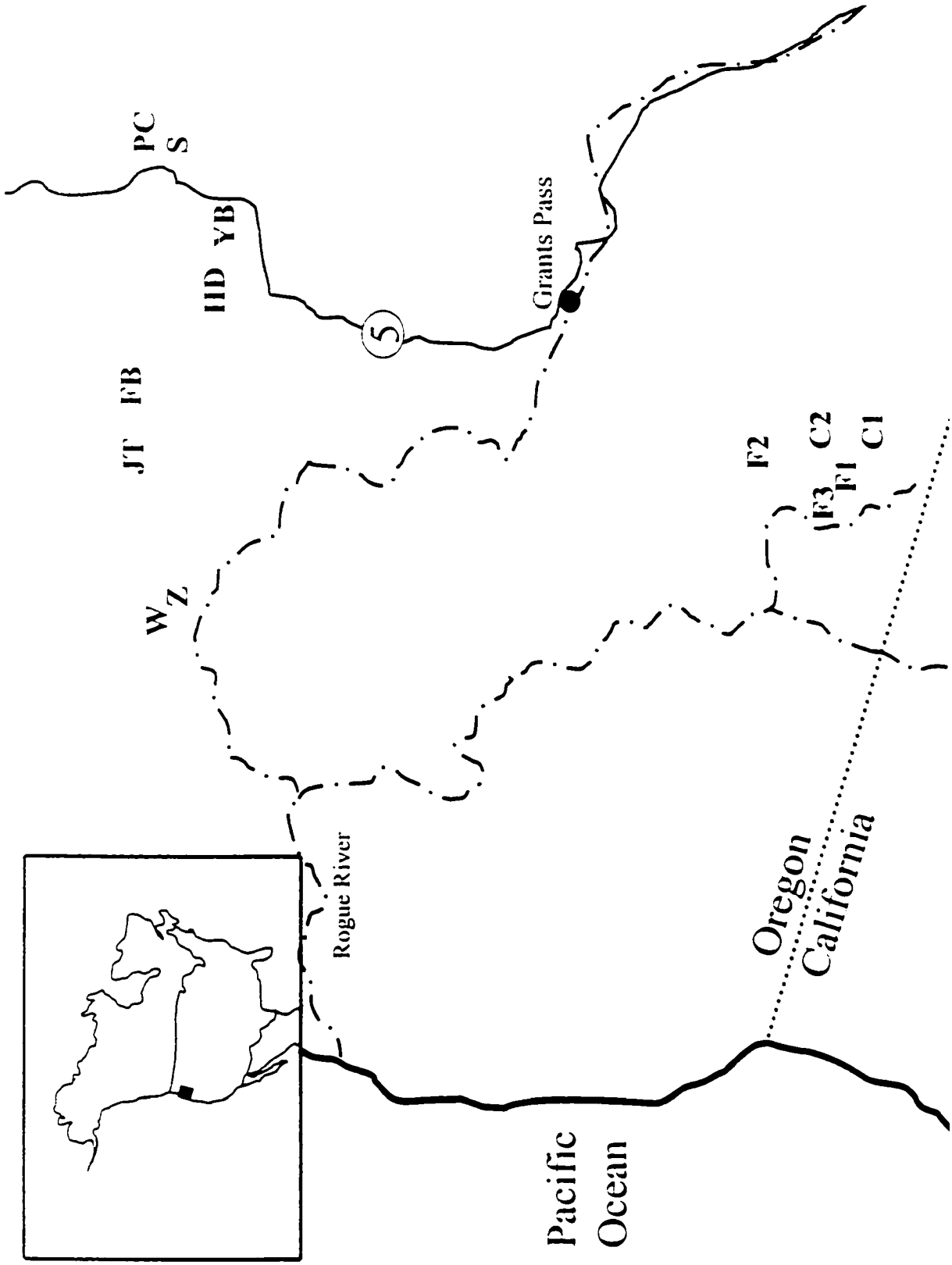
	1998				1999			
Site	1	2	3	4	1	2	3	4
F1	21, 17	24, 20	22, 21	20, 17	13, 22	15, 10	6, 16	13, 14
	38	**44**	**43**	**37**	**35**	**25**	**22**	**27**
F2	9, 9	9, 13	12, 18	15, 18	20, 16	11, 7	13, 9	7, 12
	18	**22**	**30**	**33**	**36**	**18**	**22**	**19**
C1	7, 4	10, 14	16, 12	15, 15	9, 17	7, 10	9, 6	5, 7
	11	**24**	**28**	**30**	**26**	**17**	**15**	**12**
C2	10, 12	22, 16	28.10, 18	31.18, 19	19, 17	16, 7	12, 7	12, 10
	22	**38**	**46.10**	**50.18**	**36**	**23**	**19**	**22**
			(0.86)	**(0.90)**				

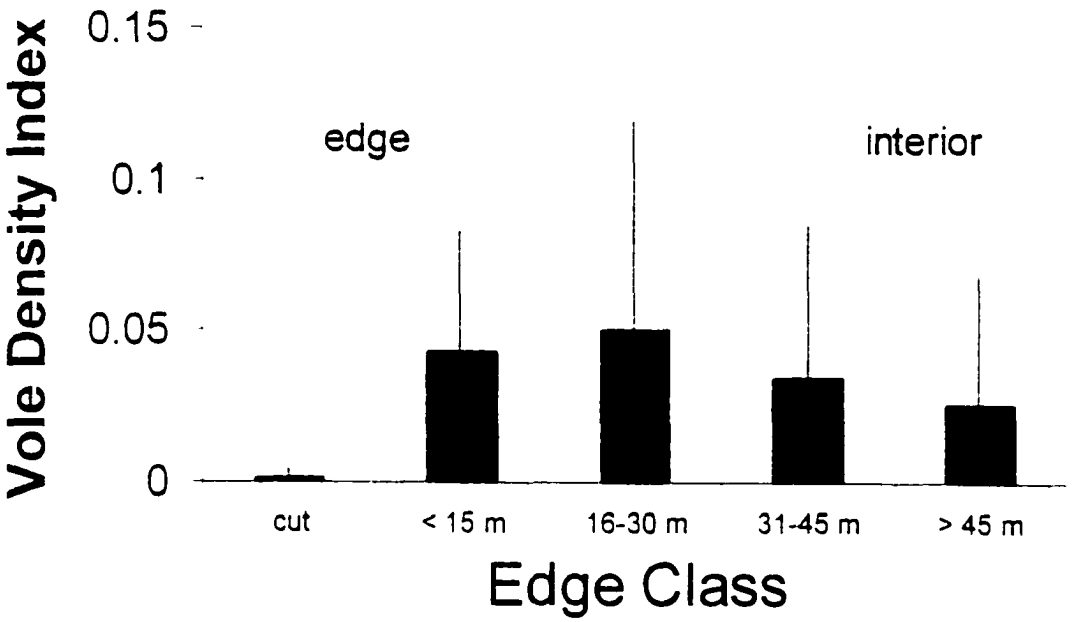
Figure 1: Map of study areas in southwestern Oregon used to investigate vole demography.

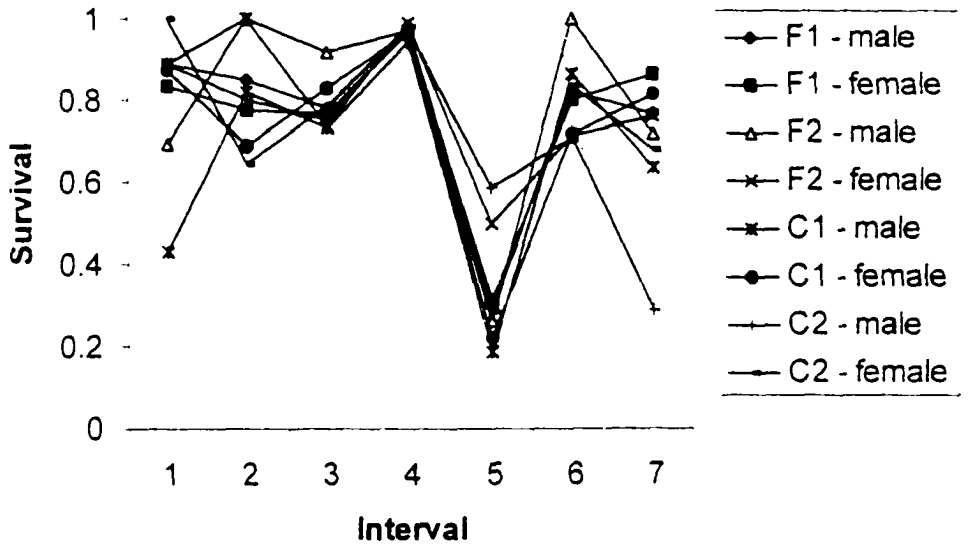
Figure 2: Mean and standard errors of vole density in clearcuts (cut) and forest fragment edge classes. Values on x-axis show the distance of traps in each edge class from the nearest forest-clearcut interface.

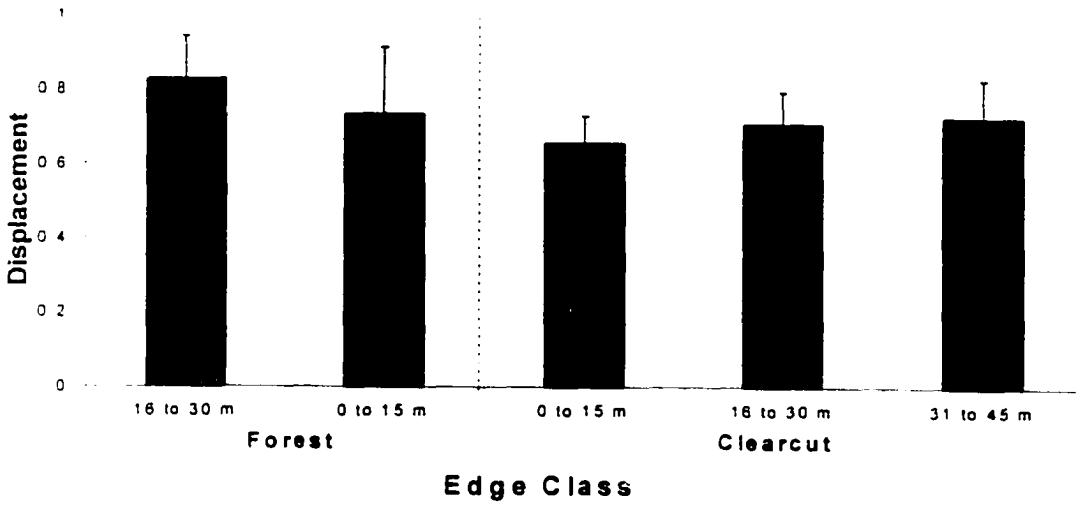
Figure 3: Adult vole survival estimates on two forest fragments (F1 and F2) and two contiguous forest control sites (C1 and C2). Each line represents the estimated survival of a sex at a site. Although the standard errors are not shown in order to make data presentation easier, they varied greatly from 0.01 to 0.18.

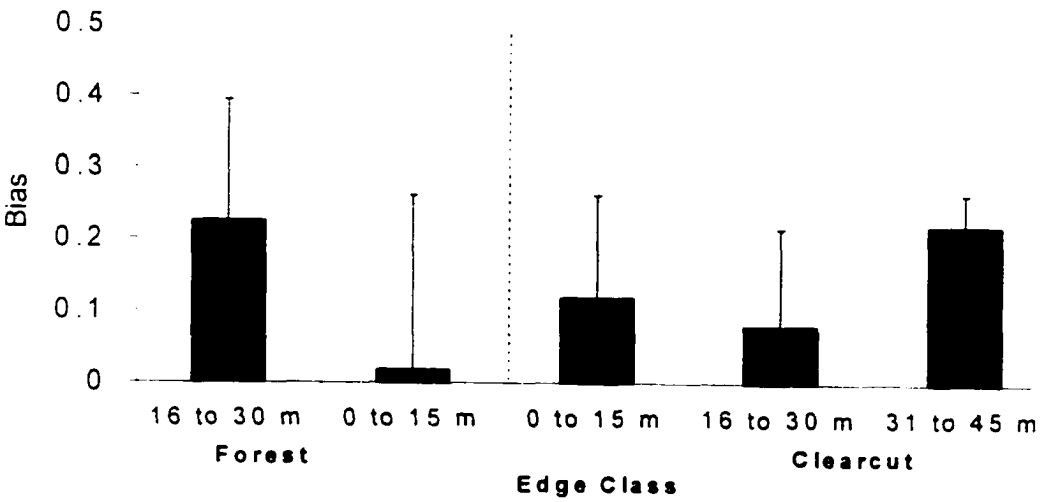
Figure 4: Movement characteristics of voles at different distances from the forest clearcut edge. Displacement shows the net linear movement per 1 m of vole path. Bias indicates the orientation relative to the forest edge. Correlation represents the directedness of successive 1 m path segments.

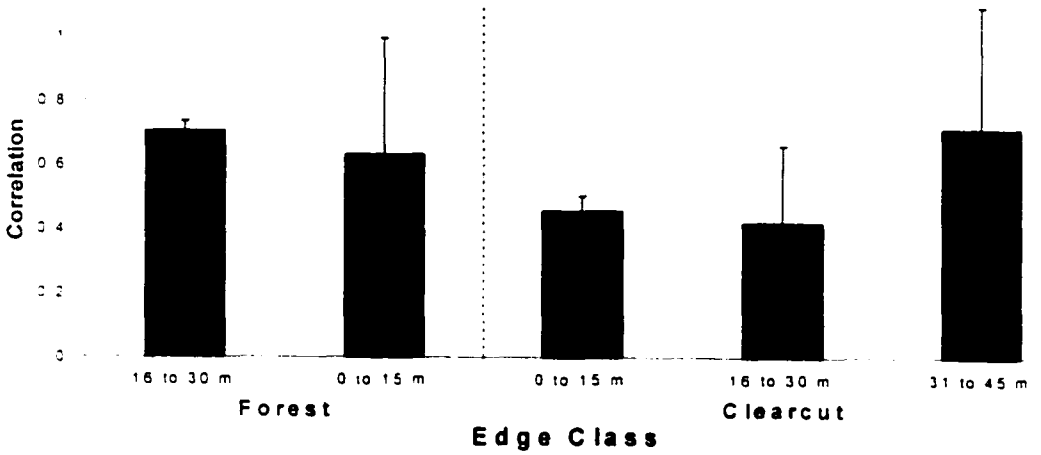












Chapter 4 - The Ecological Role of Voles as Dispersers of Ectomycorrhizal Fungi

ABSTRACT

The formation of ectomycorrhizae on seedlings is thought to be important to successful re-establishment of conifers in clearcut areas. However, many ectomycorrhizal fungi are dependent upon small mammals for dispersal. I investigated the potential of California red-backed voles (*Clethrionomys californicus*) and deer mice (*Peromyscus maniculatus*) to inoculate seedlings with ectomycorrhizae by placing vole and mouse feces on seedlings grown under water stress in clearcut soil. The seedlings in each treatment did not differ in terms of mycorrhizal fungi diversity, number of root tips, or growth rate. These results suggest that the hypothesized role of small mammals as dispersal vectors for important fungi may be compromised under the stressful conditions experienced by conifers in clearcuts.

INTRODUCTION

Many ecologists have recently revised their views of how plant communities are structured. This revision includes a less extreme emphasis on the role of abiotic conditions and competition among plants as the primary determinants of plant community structure, and the inclusion of an important role for positive interactions among plants (Callaway and Walker 1997). In addition, increased appreciation of the importance of positive interactions has been expanded from plant-plant interactions to cross divergent taxonomic lines and include plant-fungus interactions (Perry et al. 1989).

Plants and fungi can form important mutualisms in which plants receive soil nutrients and water in exchange for carbon donated to fungi (Hartnett et al. 1993). By forming mutualisms, mycorrhizae can affect the outcome of plant-plant and plant-microbe competitive interactions (Hartnett et al. 1993, Kaye and Hart 1997, Simard et al. 1997). Ectomycorrhizal fungi (EMF) also increase lateral root growth and increase survival, growth and competitive abilities of host plants (Castellano and Trappe 1985, Perry et al. 1987). In the Pacific Northwest of the US, all conifers form mycorrhizae and this relationship is thought to be very important to the health of Northwest forests (Perry et al. 1989).

Added to the apparent mutualism between many trees and EMF is another layer of complexity, the role of mycophagous small mammals. It has been suggested that small mammals may serve a critical role as dispersers of EMF. Many EMF species produce fruits below ground (hypogeous sporocarps) and, consequently, are thought to be dependent upon mycophagous mammals for dispersal. It has been shown that the germination rate of some EMF spores can be increased by passage through small

mammals (Kotter and Farentinos 1984, Cork and Kenagy 1989, Lamont et al. 1985). Consequently, there is a potentially important web of interactions among plants, mycorrhizal fungi, and small mammals.

Experimental research has shown that small mammals can decrease the biomass of fungal sporocarps in Pacific Northwest forests, indicating that they are important consumers of EMF (North et al. 1997). The California red-backed vole (*Clethrionomys californicus*) has a specialized diet of hypogeous EMF sporocarps (> 80% of diet by volume; Maser et al. 1978, Ure and Maser 1982, Hayes 1986). Although no experimental work has been conducted to better define the relationship between the California red-backed vole and hypogeous EMF, available evidence suggests voles may be important dispersers of hypogeous EMF (Maser et al. 1978). The closely related southern red-backed vole (*Clethrionmys gapperi*) has been shown to be a potential dispersal vector for hypogeous EMF in Minnesota forests (Terwilliger and Pastor 1999).

Coniferous forests of the Pacific Northwest are highly disturbed. It has been estimated that approximately 85% of original old-growth Douglas fir forests in Washington and Oregon have been lost, mostly by clearcutting (Booth 1992). Remaining forests are highly fragmented into a mosaic of old forests in a matrix of clearcuts and young, regenerating forests. Clearcuts in southwestern Oregon are extremely hot and dry and are slow to regenerate into coniferous forests (Minore 1986). It has been shown that clearcuts and young regenerating forests have reduced ectomycorrhizal diversity (Durall et al. 1999, Hagerman et al. 1999) and truffle biomass (North et al. 1997, Amaranthus et al. 1994, Clarkson and Mills 1994) relative to mature forests, which may hinder regeneration of conifers. In our study area, some clearcuts fail to support conifers even

after multiple attempts to re-plant them and can be overtaken by shrubs and grasses (Perry et al. 1987, 1989).

California red-backed voles are rarely trapped in clearcuts (Tevis 1956, Gashwiler 1959, Mills 1995, Tallmon et al. in prep), but are known to disperse through clearcuts (Tallmon et al. submitted). This begs the question of whether or not voles, which are highly mycophagous, but rarely found in clearcuts, could effectively inoculate clearcuts with ectomycorrhizal spores during dispersal events and increase conifer survival. In contrast to voles, deer mice (*Peromyscus maniculatus*) are commonly found in clearcuts and adjacent forest (Mills 1996). Although they appear to consume EMF only opportunitistically (Fogel and Trappe 1978), they could also be effective inoculators of clearcuts with EMF because they are abundant and commonly move between clearcuts and adjacent forest where EMF sporocarps are more abundant (Tallmon et al. in prep).

In this study, we experimentally examined the importance of voles and mice to EMF formation and growth of seedlings in clearcuts. We planted Douglas-fir (*Pseudotsuga menzesii*) seedlings in soil collected from recent clearcuts in southwestern Oregon. These seedlings received treatments of vole feces, autoclaved vole feces, mouse feces, or no feces (control). The seedlings were subjected to water stress to simulate conditions in the hot, dry clearcuts of southwestern Oregon. This approach allowed us to investigate the potential positive effects of small mammals on seedlings by determining whether they might increase the EMF formation and growth of conifer seedlings in highly disturbed clearcuts.

MATERIALS AND METHODS

Feces

Fecal pellets were obtained from California red-backed voles and deer mice live-captured at sites in southwestern Oregon in the summer of 1998 as a part of a study on the effects of forest fragmentation on small mammal demography and genetics (Tallmon et al. submitted). Feces were collected directly from individual animals with forceps and placed in 1.5 ml microfuge tubes. These tubes were then frozen until application on the tree seedlings. Ten of these samples were randomly sampled and investigated under a microscope for spore diversity following Colgan (1997) and Castellano (1989). Each sample contained spores from three to seven genera of EMF and collectively contained spores from a wide variety of genera, including: *Rhizopogon*, *Hysterangium*, *Martellia/Gymnomyces*, *Glomus*, *Elaphomyces*, *Gautieria*, *Leucophleps*, *Geopora*, *Genabea*, *Picoa*, and *Hydnotrya*.

Seedlings

Douglas-fir seeds were obtained from the USDA Stone Nursery (Jacksonville, OR) in February 1999. On February 25, 1999, seeds were placed on paper towels wetted with 5% Captan solution. These were placed in plastic bags and refrigerated until April 21st. Next, these seeds were placed in sterilized plastic containers (deepots) containing an autoclaved 50:50 mixture of perlite and vermiculite and kept in an isolated growth room with artificial light. The seeds germinated in the next week and were watered every two or three days. On May 29th, the resulting seedlings were then moved to Cave Junction, Oregon, where they were kept outside in a shaded area.

On June 25th, the total length of each seedling was measured and each seedling was replanted in larger plastic containers with topsoil randomly assigned from one of three clearcut sites. The clearcuts had been cut in and burned in 1997 as a part of the Buckhorn Ridge Timber Sale on the Illinois Valley Ranger District. After two weeks, the seedlings in each of the three topsoil treatments were randomly assigned one of three fecal treatments or a control (plus an additional 1-2 cm^3 of the appropriate clearcut topsoil): 1) 3-5 vole pellets; 2) 3-5 autoclaved vole pellets; 3) 3-5 mouse pellets; 4) soil only. The seedlings were watered immediately after the application of the fecal treatments.

On August 18th, 1999, the seedlings were moved to Missoula, MT, where they were kept outdoors until November 18th. The seedlings were then kept indoors under a window that provided natural light until April 11th, 1999 when they were harvested and measured. The seedlings were watered once or twice per week after receiving both treatments to simulate the water stress placed on seedlings in clearcuts in southwestern Oregon. Although this is more regular pattern of watering than plants receive in the field, because the deepots have a small volume and do not store moisture for long periods of time, the seedlings were often in dry soil.

Measurements and Statistical Analysis

Ten seedlings from each treatment combination were measured for the presence of ectomycorrhizae, the number of different mycorrhizal types colonizing the roots, and the number of root tips. The total length (mm) was also measured for twenty seedlings from each treatment. A Chi-square was used to test for differences in the presence of

ectomycorrhizae. The distributions of the other variables were tested for normality using a Wilk-Shapiro test and their means were compared among treatments using a two-way ANOVA.

RESULTS

There was no effect of fecal treatments upon the response variables we measured. The number of seedlings that formed mycorrhizae was not greater in the vole treatment ($F = 4.65$, $p > 0.05$). Of those seedlings with mycorrhizae, all were colonized only the brown or MRA mycorrhizae type, except for one seedling in the vole treatment with site 1 soil that was also colonized by *Rhizopogon*. Clearly, the diversity of mycorrhizae on seedlings was not increased in any of the treatments relative to the control with no fecal application. The number of root tips differed somewhat among fecal treatments, but not significantly ($F = 2.20$, $p = 0.0923$) and was not greater in the vole fecal treatment (Figure 1). Similarly, seedling growth was not different among fecal treatments ($F = 1.60$, $p = 0.1929$; Figure 2). In contrast to the fecal treatments, there was a significant effect of soil origin on the number of root tips and seedling growth. Seedlings grown in soil from site 1 showed a larger number of lateral roots ($p = 0.0027$) and had greater growth ($p = 0.0016$) than seedlings from the other sites. There were no significant interactions between the soil and fecal treatments.

DISCUSSION

We found no evidence that California red-backed voles or deer mice improve the fitness of seedlings grown in stressful conditions by inoculating them with EMF.

Seedlings given vole or mouse fecal treatments did not show higher rates of EMF colonization, greater EMF diversity, a greater number of root tips, or faster growth. This lack of any difference in EMF diversity among fecal treatments in fitness traits is surprising, because a sample of the feces used in this study are known to have contained a wide variety of EMF spores. Further, the lack of any EMF diversity at all (except for a single seedling that showed both the brown and *Rhizopogon* types) is surprising, because seedlings were grown outdoors for part of this study and could have been colonized by wind-carried EMF spores. There greater number of root tips and growth rate of seedlings grown in soil from Site 1 are likely due to the smaller proportion of rocks in the soil from this site, which probably allowed the seedlings in this soil to obtain more moisture during the study.

In southwest Oregon, clearcuts are often hot and dry during summer months (Minore 1986, Perry 1989). In areas where coniferous forests have been clearcut, it has been shown that EMF biomass and diversity decrease at increasing distances from forest edges (Hagerman et al. 1999, Durall et al. 1999). In southwest Oregon, some clearcuts soils near our sites have been found to be bereft of mycorrhizal fungi hyphae within a year following tree harvest (Perry et al. 1987). Because conifer seedlings obtain needed amounts of important resources more quickly by forming ectomycorrhizae than without ectomycorrhizae, the loss of EMF in clearcuts is an important concern for re-forestation efforts (Perry et al. 1989).

Previous authors have suggested that mycophagous small mammals, such as the California red-backed vole, may play an important role in the dispersal of EMF (Maser et al. 1978). It has been shown that southern red-backed voles can increase the diversity

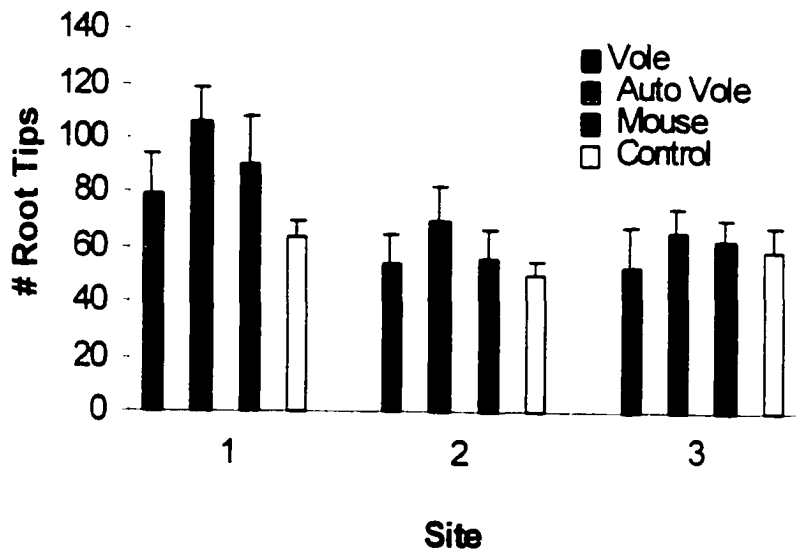
and colonization success of EMF on seedlings grown in beging greenhouse conditions (Terwilliger and Pastor 1999). Small mammals are capable of dispersing through clearcuts and can deposit many different genera of EMF in their feces, so they could effectively inoculate multiple locations in clearcuts with EMF during a single dispersal event. Under the stressful conditions in clearcuts simulated in this study, we found no evidence that California red-backed voles or deer mice are potentially important dispersal vectors of EMF spores. In addition, there was no evidence that wind-carried EMF spores successfully colonized these conifers. This suggests that the stress experienced by conifer seedlings may simply prevent EMF formation.

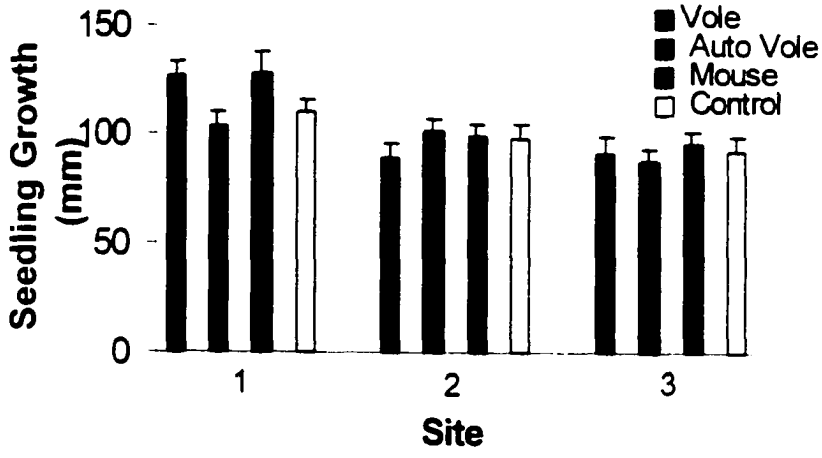
There are alternative sources of EMF for conifer seedlings in clearcuts. EMF could be obtained by seedlings from hardwood trees that are generally more tolerant of abiotic conditions in clearcuts (Minore 1986). Hardwood trees in clearcuts harbor some EMF that can also colonize conifers (Borchers and Perry 1990, Molina et al. 1997, Massicotte et al. 1999). Because EMF associated with multiple hosts can move important nutrients between hosts (Simard et al. 1997), healthy hardwoods may actually support the succession of conifer seedlings in clearcuts by directly supplying them with nutrients via fungal mycelia and by providing shade.

Based on the results of this study, hardwood trees may be a much better source of EMF for conifer seedlings in clearcuts than are small mammals. In this study, we found no evidence to suggest that small mammals or wind are sufficient vectors to inoculate seedlings with EMF when seedlings are grown under stressful conditions that mimic those found in clearcuts.

Figure 1: The mean (and SE) number of root tips on Douglas fir seedlings grown in soil from clearcuts in southwestern Oregon.

Figure 2: The mean (and SE) growth of Douglas fir seedlings grown in soil from clearcuts in southwestern Oregon.





Chapter 5 - The Rise of Mice and the Fall of Trillium in a Fragmented Landscape

ABSTRACT

We investigated how forest fragmentation has changed deer mouse *(Peromyscus maniculatus*) population dynamics and the effects of these changes on recruitment in the understory plant trillium (*Trillium ovatum*). Multi-state demographic modelling of mark-recapture data showed that deer mouse survival is highest in clearcuts, lower in forest fragments, and lowest in contiguous forests and that movement among these habitats is common. Collectively the survival and movement rates led to higher deer mouse densities at forest fragment sites than in control (unfragmented) sites. Trillium seeds in experimental trials were more likely to be predated in areas of elevated relative mouse abundance than in areas of lower relative abundance, supporting previous suggestions that deer mice increase extinction risks for trillium populations in fragmented forests. Positive effects of forest harvest and fragmentation on deer mice are likely to have important implications for the population dynamics and the distribution of understory plants that produce seeds susceptible to mouse predation.

INTRODUCTION

Landscape-level studies have recently gained prominence in ecology. This shift to large-scale ecological studies has been motivated by the vast scale at which humans have fragmented natural habitats and understanding that migration among populations plays a critical in the evolution (Wright 1931) and short term dynamics (Pulliam 1988, Wootten and Bell 1988) of wild populations. Despite the broad geographic focus now embraced by many ecologists, a large hole in our understanding of population responses to fragmentation at a landscape level persists due to technical challenges in linking population dynamics in different habitats within a landscape. That is, the difficulties of measuring movement among populations have limited most studies of wild populations to estimating demographic rates from single habitat types (Koenig et al. 1996). Few studies have quantified how migration among different habitats or populations might affect local population dynamics (but see Spendelow et al. 1995, Lindberg et al. 1998, Lair et al. in prep). Improved understanding of population dynamics in individual habitats and movements among these habitats in important not only for insights into single species, but also because population-level changes for single species can cascade into multiple effects on community dynamics (Crooks et al. 1999).

In forests of the Pacific Northwest, like many forests throughout the world, a majority of structurally and biotically diverse old-growth forests have been harvested and converted into single-species monocultures of even-aged and even-sized trees that differ in many physical and biotic characteristics (Garman et al. 1999, cite Amazonia stuff). Negative ecological effects of forest harvest and fragmentation include altered tree mortality, recruitment, growth and species composition along forest edges (Chen 1992),

increased isolation for some species in habitat fragments (Mills 1995), and the decline of old-growth dependent species such as the Northern spotted owl (*Strix occidentalis caurina*; Lande 1988).

One species that has received considerable research attention in Pacific Northwest forests is the deer mouse (*Peromyscus maniculatus*), largely because it is known to be a generalist seed predator and thought to be the most important inhibitor of re-seeding efforts in clearcuts (Banfield 1974). Despite a large economic interest in understanding how forest harvest practices affect deer mice and how deer mice, in turn, affect tree recruitment in clearcuts, existing studies have not reached a consensus on the impacts of clearcutting on deer mouse population dynamics. Some studies have found a positive effect of clearcutting on deer mouse populations (e.g. Hooven and Black 1976, Tevis 1956, van Horne 1981), whereas other have found no effect (Petticrew and Sadleir 1974, Sullivan 1979). In a study that included some of our research sites, Mills (1996) found a positive effect of edge on the relative abundance of mice.

It is important to determine how forest fragmentation effects on deer mouse demography because changes in deer mouse population dynamics may include negative indirect effects on herbaceous plants. Jules (1998) and Jules and Rathcke (1999) counted the annual growth constrictions on trillium (*Trillium ovatum*) rhizomes and found that reduced recruitment following clearcutting increased extinction risk for trillium populations near forest fragment edges and in clearcuts. Further, trillium recruitment in forest fragment populations decreased with proximity to forest/clearcut edge. A series of manipulative studies suggested that reduced recruitment along forest fragment edges was caused by either increased seed predation by rodents or altered pollination.

We used a mark-recapture approach to examine the effects of forest fragmentation on deer mouse population dynamics in southwestern Oregon and experimental seed trials to investigate the effects of deer mice on trillium recruitment. We sought first to determine whether or not habitat fragmentation has led to quantifiable changes in the apparent survival and movement of adult deer mice in the different habitats common to fragmented forests of the Pacific Northwest -- clearcuts, forest edges, and forest interiors. We also used the empirically derived adult survival rates in a deterministic matrix projection model to infer how different habitats could be expected to affect population growth, and compared these expectations to densities of mice on all of our sites. Finally, we sought to determine whether or not trillium seed predation is elevated in areas of higher mouse abundance. The potential landscape level implications of this work are vast because half of the old-growth Douglas-fir forests in the Pacific Northwest have been harvested, mostly by clearcutting, and a large proportion of remaining forests are interspersed with young tree plantations (Garman et al. 1999).

MATERIALS AND METHODS

Site Descriptions and Trapping Protocols

During the summers of 1998 and 1999, we trapped mice at five sites in the Sucker Creek drainage of southwest Oregon. All sites are dominated by Douglas-fir (*Pseudostuga menzesii*) trees and have herbaceous understories. Three sites are forest fragments completely surrounded by clearcuts logged between 1964 and 1987: F1 (3.0 ha), F2 (3.7 ha), and F3 (0.5 ha). F1 and F3 are separated by a common clearcut. F1, F2, and F3 were used by Mills (1995, 1996; named E, O, and M, respectively), and F1 and F2

were used by Jules (1998; named I and II, respectively) in previous studies of the ecological effects of habitat fragmentation. We completely covered each fragment with a grid of traps spaced at 15 m intervals, and surrounded each fragment with 4 transects of 6 traps each, placed 50 m into the clearcut from the forest edge (Figure 1). The number of traps on each fragment was 122 (F1), 154 (F2), and 21 (F3).

We used the same grid and peripheral transect configuration to trap two control sites, C1 and C2, located in continuous forest >150 m from the southern and northern borders of Oregon Caves National Monument. Each control site consisted of 102 traps, spaced 15 m apart in a 17 x 6 grid, plus 4 surrounding transects of 6 traps each set parallel to each edge of the grid and 50 m away from the grid. The 4 peripheral transects around the control grids were analagous to the clearcut traps around the fragment grids, and we refer to them as the control "periphery" (Figure 1).

During four trapping sessions each summer we uniquely marked all deer mice captured at each site. Each trapping session lasted four consecutive nights, except for the first trapping session of eight consecutive nights. All 4 sessions each summer were separated by a 16-day interval, except for the first and second sessions of 1998, which were separated by 20 days. Each evening of each trapping session, we baited small Sherman live traps with oat groats, sunflower seeds, 1 cm^3 of fresh apple, and polyester batting, and then placed each trap inside a pint milk container lined with batting. We checked and closed all traps each morning to minimize mortality.

Apparent Survival and Movement

We examined variation in deer mouse survival and movement within continuous forest, and among forest fragment interior, forest edge, and clearcut habitats using a multi-state modeling approach (Hestbeck et al. 1991, Brownie et al. 1993, Nichols and Kendall 1995). To do this, we assigned each trap at each site to one of six states, or "habitats". At forest fragment sites, we assigned each grid trap within 30 m of the forest edge to the fragment edge habitat. We assigned all grid traps located >30 m from the fragment edge to the fragment interior habitat and all traps in the clearcut transects to the clearcut habitat. We superimposed analogous habitat types, or states, on the trapping grid at the control sites following the criteria used on fragments. We assigned traps < 30 m from the outer traps of the trapping grid to the control edge and assigned all other grid traps to the control interior. We assigned the traps in transects surrounding each grid to the control periphery, just as the traps in transects surrounding the fragments were assigned to the clearcut.

Each time a mouse was trapped, we recorded the habitat -- clearcut, fragment edge, fragment interior, control periphery, control edge, control interior – in which it was captured. For cases in which we captured a mouse in two habitats in a single trapping session, we assigned it to the last habitat in which it was captured. Thus, we consolidated the capture histories of all individuals to a maximum of a single capture for each session for the analysis of survival and movement.

In order to address our questions relating to deer mouse demography, we developed a set of 15 candidate models that we thought provided realistic approximations of the underlying dynamics of the study populations based upon our field observations.

These models consisted of different combinations of temporal and habitat specific variation in apparent survival (Φ), movement (Ψ), and apparent capture (p) probabilities. Apparent survival, movement, and capture probabilities are defined as the probabilities of survival, movement, and capture for individuals that do not permanently emigrate from the study sites. Because we were interested in the effects of the different habitat types on survival and movement, we pooled data across sites for each habitat type and across sexes. This allowed us to reduce the number of parameters in each model and the number of different models we had to compare. Consequently, the temporal component consisted of variation in Φ, Ψ, and p between capture sessions. And, the habitat component consisted of variation in these parameters among the three fragment habitats and among the three control habitats.

We examined all candidate models with the mark-recapture program MARK (White and Burnham 1999) using a modified step-down approach (see Lebreton et al. 1992, p. 84). Essentially, we varied the parameter of least interest, p, until the optimal parameterization of p was found, and then continued on to investigate Ψ, and then Φ. After the first 15 pre-conceived models were run, we examined a few more models with less optimal parameterizations, to ensure we had not settled upon a bad approximating model (Table 1). MARK provides Akaike's Information Criteria (AIC) to assess the fit of the candidate models to the underlying population dynamics that generated the data. AIC is a parsimony-based approach that has become the standard means to quantitatively rank mark-recapture models (White and Burnham 1997). The model with the lowest AIC value is the one that most adequately describes the variation in the underlying population

dynamics without including so many parameters such that the precision of parameter estimates is sacrificed.

Stage-based Projections

We explored how differences in adult survival among habitats might affect population growth rates with habitat-specfic matrix projection models. We used published estimates of mouse fecundity, juvenile survival, and the proportion of breeding adults from other studies, along with the habitat-specific adult survival values from our study, to complete a stage-based matrix projection model of mouse life history for each habitat (Appendix). This allowed us to explore the biological significance of observed differences in adult survival. That is, we could assess how changes in adult survival rates across clearcuts, the forest fragment edges and interiors, and contiguous forest would be predicted to impact population dynamics by examining habitat-specific growth rates.

Density Estimates

To determine whether or not differences in habitat-specific survival may translate into differences in density between fragment and control sites, we estimated mouse density at each site by dividing the abundance of mice by the effective trapping area. This required that we input all mark-recapture data collected at each site in the last trapping sessions of 1998 and 1999 into MARK to generate closed-capture model estimates of abundance (Table 2). As with the multi-state models, we first developed a set of candidate models thought to provide realistic approximations of mouse biology and compared them using AIC values.

The effective area trapped at each site was estimated following Wilson and Anderson (1985) and Nichols and Karanth (1998). We first summed the area covered by the trapping grid and the area between the trapping grid and peripheral transects (shaded area, Figure 1). Then, we used the mean maximum distance moved by individuals at each site to estimate a boundary width. This boundary width was then multiplied by the perimeter of the region outlined by the trapping grid and peripheral transects to determine the effective trapping area.

Seed Predation Experiment

In August 1999, we used seed trials to investigate how changes in mouse demography mice affect trillium seed predation rates. First, we made seed platforms by driving a ~20 cm long nail through each of 22 10 cm x 10 cm pieces of plywood. Then, we identified the two trap stations in each of the 11 clearcut transects surrounded the fragment sites that had the highest and lowest mouse capture rates. We staked a platform ~10 cm off the ground, 5 m to either side of the "high" and "low" trap station in each transect. We then coated each nail with Tanglefoot® (Tanglefoot Co., Grand Rapids, MI, USA) to prevent ants from ascending the platform. Finally, we placed five trillium seeds on both of the platforms at each station and randomly chose one of the two platforms to serve as a control. The control was then covered with a strawberry basket to exclude mice.

We conducted our seed trials between trapping sessions. Platforms were set for five consecutive nights, but we conducted seed trials only on the first, third, and fifth nights. In each trial, we placed five seeds on each platform at dusk and then returned the

following dawn to count the number of seeds removed, to remove remaining seeds, and to subtract any seeds removed from each control platform from the number predated from the adjacent treatment platform. We used a paired t-test to compare the arcsine square-root transformed proportion of seeds predated at the trap stations in each clearcut with the highest and lowest mouse capture rates. Linear regression was used to explore the effects of relative mouse abundance on seed predation across all stations.

RESULTS

Survival and Movement

A total of 377 individual deer mice were captured at these sites in the summers of 1998 and 1999. However, 37 individuals first captured in the last session of 1999 were removed from this data set because they could not be used to investigate movement or survival. Of the remaining 340 mice, 295 were captured at the fragment sites and 45 were captured at the control sites. After collapsing the data to no more than a single capture per individual per trapping session, 710 captures were used to investigate deer mouse movement and survival.

Ultimately, the best supported models of the candidate set were those that included habitat-specific survival and movement estimates for each of the three fragment habitats and only a single survival and movement estimate for all three habitats superimposed on control sites. In other words, the data supported habitat-specific survival and movement estimates for fragment habitats, but did not support habitat-specific estimates for control habitats. Two models received much greater support than all others (Table 1). These models provided nearly identical estimates of survival and

movement, so only results from the best-supported model are presented. In this model, adult survival was highest in clearcuts (Φ = 0.87; SE =0.02), intermediate in forest fragment edges (Φ = 0.78; SE = 0.03) and interiors (Φ = 0.77; SE = 0.05), and lowest in contiguous forests (Φ = 0.61; SE = 0.06). There was little evidence that survival differed between fragment edges and interiors, since the point estimates for these two habitats are nearly identical and the SE's overlap greatly. However, differences in survival between these two habitats were clearly intermediate between survival in the clearcut habitat and the control sites. Interestingly, all 12 individuals captured in 1998 that survived to be recaptured in 1999 were from the edges and clearcuts of fragment sites; none from forest interiors or the control sites were recaptured in the 1999 field season.

Movement rates among the fragment habitats also provide insight into the demography of mice in this fragmented landscape. Movement rates were generally high, though there was both a distance effect and a habitat effect upon movement rates at fragment sites (Figure 3). First, movement rates were greater between adjacent habitats than between distant habitats. For example, movement from the clearcut to the edge was much higher (Ψ = 0.14 (SE 0.03)) than from the clearcut to the interior (Ψ = 0.02 (SE 0.02)). In addition, the fragment interior habitat had much higher emigration rates than the other habitats. However, there were fewer mice captured in the fragment interiors than edges and clearcuts each session. Consequently, the absolute number of mice emigrating was not that different among fragment habitats. In contrast to the fragment habitats, only a single movement rate 0.25 (SE 0.07) between all control habitats was supported by the data.

Survival and movement estimates were precise because of high capture probabilities at fragment sites. Although capture probabilities varied across strata at the fragment sites and between the fragment habitats and the control, the highest estimate of p =1.00 (SE 0.00) in the clearcut habitat and the lowest estimate of p = 0.89 (SE 0.03) in the fragment interior habitat are both quite high. We captured nearly all marked individuals that did not permanently emigrate each trapping session, which led to small standard errors around survival and movement estimates, despite a relatively small total number of mice captured.

Population Growth Rates

The four different apparent survival estimates for adult mice from the three fragment habitats and the controls had dramatically different effects on otherwise identical population projection matrices and suggest a dramatic positive effect of forest fragmentation on deer mice (Table 3). Projected population growth in the project matrix using adult survival values from the clearcut habitat was 1.17, which contrasted greatly with the lowest value of 0.78 found in controls. The population growth rates from the fragment edge and interior habitats were intermediate with 1.03 and 1.00, respectively.

Densities

Deer mouse densities were higher at the fragment sites than at the control sites in 1998 and 1999 (Table 4). In 1998, mouse densities at fragment sites ranged from approximately 7 -13 mice per 10,000 m^2. These densities are roughly three times greater

than on controls. In 1999, mouse densities were lower across all fragment sites, but mouse densities were still four times higher at fragment sites than at control sites.

Trillium Predation

We found a strong, positive relationship between deer mice and trillium seed predation (Figure 4). Seeds located in areas of higher mouse abundance suffered higher predation rates than those located in areas of lower mouse abundance (t = 3.20; p = 0.0094; $d.f.$ = 10). In addition, 32% of the variation in seed predation was explained by differences in the relative abundance of mice across trapping stations (r^2 =0.32; p=0.003; $d.f.$ = 21).

DISCUSSION

Habitat fragmentation has led to quantifiable changes in the physical environment of Pacific Northwest forests (Chen 1992). It follows that these changes should alter demographic rates and population dynamics for many forest animals and result in cascading trophic effects. Surprisingly, there are few examples that demonstrate these patterns and, in the case of deer mice population dynamics, different studies tend to present conflicting conclusions on the effects of forest fragmentation. We found strong positive effects of clearcuts and forest fragments on deer mouse population dynamics and important ecological consequences of these changes.

Our data show clear habitat-specific effects of fragmentation on adult deer mouse apparent survival, and that deer mice move freely among habitats. Adult survival was much higher in clearcuts than forest fragment edges and interiors, and survival was

greater in all of these habitats than in continuous forests. At fragment sites, deer mice appeared to move at fairly high rates between fragment edges, interiors, and clearcuts (Figure 3). Within a single generation, individual mice moved across multiple habitats within a given site. Accordingly, positive effects of one habitat type on deer mouse fitness will affect deer mouse population dynamics in nearby habitats. Movement among habitats has not been considered in previous studies of deer mice in fragmented forests, even though long-distance dispersal has been documented (Van Horne 1981).

The use of survival rate estimates from our field sites in projection models showed that clearcuts may serve as a demographic source for deer mice. Previous studies show that adult survival was the most important vital rate in terms of explaining variation in deer mouse population growth rates (Citta 1996). So, it is not surprising that differences in adult survival in clearcuts and contiguous forests resulted in dramatic differences in projected growth rates between the clearcuts and contiguous forests. Because we had to rely on juvenile survival and fecundity values from different studies in our population projection matrices, the relative differences in population growth rate among habitats are much more important than the absolute differences among habitats. In fact, the absolute growth rate estimates are very likely to be wrong. Nonetheless, the results show a clear and positive effect of clearcutting and habitat fragmentation on adult survival, which translates into a large impact on population growth rates in altered habitats. If other vital rates are not strongly compensatory or otherwise very different among habitats, then the increased fitness of mice in clearcuts will impact other habitats.

Ultimately, it would be most useful to directly estimate population growth rates in different habitats directly from mark-recapture based recruitment estimates (Pradel 1996).

Unfortunately, this approach is so data intensive that it is difficult to obtain population growth rate estimates that are precise enough to be biologically informative, even for well-studied species such as Northern spotted owls *(Strix occidentalis caurina*: Franklin et al. in press). However, as in our study, the use of a mark-recapture approach will necessitate a trade-off in the number of study sites in exchange for adequate data to examine details about population dynamics.

The densities of mice at each site follow what would be predicted from the field data and projection models. Densities of mice were at least two to four times higher at fragment sites than at control sites late in the breeding season. This implies the positive effects of fragmentation on survival translate into elevated densities of mice in fragmented areas. It is also important to note that the density estimates were made at the height of trillium seed set, so mouse densities are high in fragmented areas at the same time this plant is producing seeds. Because forest fragmentation has occurred on such a vast scale in the Pacific Northwest due to industrial forest harvest practices of the past century, it is likely that deer mice are much more common on a local, landscape, and regional scale than ever before.

Jules (1998) and Jules and Rathcke (1999) found that trillium recruitment was virtually absent from clearcuts and greatly reduced along the edges of forest fragments. Importantly, they were also able to show that the failed or greatly reduced recruitment in these populations corresponded to the timing of clearcut logging. Further, their results implied that deer mouse might be responsible for this reduced recruitment. These results, combined with our experimental study of trillium seed predation, provide strong evidence that forest harvest effects on deer mice has have resulted a negative effect in trillium

recruitment. We found that higher relative abundances of mice resulted in increased trillium seed predation. Although we cannot be certain that all seeds removed in our trials were predated by mice, several lines of evidence support this. First, seed predation experiments were conducted at night when most other potential predators or dispersers are inactive. In addition, mice comprised over 95% of all captures in traps placed in clearcuts, which suggests that other rodents did not greatly influence our seed trials. Finally, we found mouse feces on three uncovered platforms from which seeds had been removed. Consequently, it appears that deer mice are an important factor both in the reduced recruitment and increased extinction risk trillium populations suffer as a result of clearcutting (Jules and Rathcke 1999).

It is tempting to extrapolate our findings to other plant species. Existing evidence suggests that many plant species in the Klamath-Siskiyou region of northwestern California and southwestern Oregon are negatively affected by clearcutting and show negative edge effects (Jules et al. 1999). Of these, plants that produce large seeds or fruits may well have lower recruitment that results from positive effects of forest harvest on deer mice. Determination of the effects of deer mice on other plants awaits experimental study, but certainly deserves attention in light of our results and the well-documented feeding habits of this seed generalist (Banfield 1974). In addition, it would be wise to investigate the relationship between mice and other trillium species that are sympatric throughout large portions of North American forest subject to clearcutting.

It is apparent that clearcutting and habitat fragmentation have led to dramatic changes in deer mouse population dynamics at out study sites. These changes are detectable in terms of vital rates that vary across different habitat types and, also, in terms

of absolute numbers of mice in fragmented and unfragmented areas. That is, deer mice show positive vital rate and numeric responses to fragmentation. This study demonstrates that if habitat-specific changes in population and community dynamics can be linked across habitats, greater understanding of the direct and indirect effects of habitat fragmentation can be gained. At our study sites, changes in the population dynamics of deer mice have led to increased extinction risk for populations of the trillium plant.

Table 1: Candidate models used to examine deer mouse apparent survival and movement in fragment (F) and control (C) sites in southwestern Oregon. Variation included in the models includes time (t) and habitat (h) specific apparent survival (Φ), capture (p), and movement (Ψ) probabilities. The $\triangle$AIC value for the best-fitting model is shown in bold.

Model						
#	Φ	p	Ψ	**Description**	# P	$\triangle$AIC
1	h*t	h*t	h*t	Φ, p, Ψ vary by habitat and time	168	307.81
2	h*t	h	h*t	Φ, Ψ vary by habitat and time; p varies by habitat	132	160.40
3	h*t	F(h) C(.)	h*t	Φ, Ψ vary by habitat and time; p fragment habitat-specific, p constant across control habitats	130	157.20
4	h*t	.	h*t	Φ, Ψ vary by habitat and time; p constant across all habitats	127	140.54
5	h*t	.	F(h*t) C(t)	Φ varies by habitat and time; p constant across all habitats; fragment Ψ varies by habitat and time; control Ψ varies by time	92	73.83
6	h*t	.	h	Φ varies by habitat and time; p constant; Ψ habitat-specific	55	57.77

#	Model Φ	p	Ψ	Description	# P	ΔAIC
7	h*t	.	F(h) C(.)	Φ varies by habitat and time; p constant; fragment Ψ habitat-specific, control Ψ constant	50	52.68
8	h*t	.	h_o	Φ varies by habitat and time; p constant; Ψ habitat-of-origin-specific	49	60.04
9	h*t	.	F(h_o) C(.)	Φ varies by habitat and time; p constant; fragment Ψ habitat-of-origin-specific; control Ψ constant	47	57.02
10	h*t	.	.	Φ varies by habitat and time; p, Ψ constant	44	96.50
11	F(h*t) C(.)	.	F(h) C(.)	fragment Φ varies by habitat and time; control Φ constant; p constant; fragment Ψ habitat-specific, control Ψ constant	36	28.46
12	h	.	F(h) C(.)	Φ habitat-specific; p constant; fragment Ψ habitat-specific, control Ψ constant	14	3.49
13	F(h) C(.)	.	F(h) C(.)	fragment Φ habitat variation, control Φ constant; p constant; fragment Ψ habitat-specific, control Ψ constant	12	0.61

#	Model Φ	Model p	Model Ψ	Description	# P	ΔAIC
14	F(h,=) C(.)	.	F(h) C(.)	fragment Φ habitat-specific (but, edge Φ = cut Φ), control Φ constant; p constant; fragment Ψ habitat-specific, control Ψ constant	13	6.37
15	.	.	F(h) C(.)	Φ constant; p constant; fragment Ψ habitat-specific, control Ψ constant	9	17.36
16	F(h) C(.)	.	$F(h_o)$ C(.)	fragment Φ habitat-specific, control Φ constant; p constant; fragment Ψ habitat-of-origin-specific; control Ψ constant	9	5.26
17	F(h) C(.)	F(h) C(.)	F(h) C(.)	fragment Φ habitat-specific, control Φ constant; fragment p habitat-specific, control p constant; fragment Ψ habitat specific; control Ψ constant	15	**0.00**
18	h	F(h) C(.)	F(h) C(.)	Φ habitat-specific; fragment habitat variation in p, control constant p; fragment Ψ habitat-specific	17	2.91
19	F(h) C(.)	F(h) C(.)	$F(h_o)$ C(.)	fragment Φ habitat specific, control Φ constant; Φ; fragment habitat variation in p, control constant p; fragment Ψ habitat-of-origin-specific, control Ψ constant	12	6.43

Table 2: Closed population models, with different constraints on capture (p) and recapture probabilities (c), used the estimate the abundance of deer mice at fragmented and unfragmented (control) sites in August of 1998 and 1999. The number of parameters (#P) and relative performance of each model (△AIC) is shown. The △AIC values for the best fitting models are in bold print.

Model	Description	# P	1998 △AIC	1999 △AIC
$p_{(\ )}c_{(\ )}$	p, c constant	6	9.96	1.01
$p_{(\ )} = c_{(\ )}$	p,c constant and equal	7	15.42	23.10
$p_{(\ )}c_{(T)}$	p constant; time trend in c	8	29.99	89.12
$p_{(t)} = c_{(t)}$	p, c equal and vary through time	9	12.46	20.67
$p_{(s)} = c_{(s)}$	p,c equal, but site-specific	9	**0.00**	23.70
$p_{(T)}c_{(T)}$	time trend in p, c	9	11.33	**0.00**
$p_{(s)}c_{(s)}$	site-specific p, c	15	4.64	6.05
$p_{(\ )}c_{(T*s)}$	constant p; site-specific time trend in c	16	56.60	98.02
$p_{(T*s)}c_{(\ )}$	site-specific time trend in p; constant c	16	39.57	70.76
$p_{(T*s)}c(s)$	site-specific time trend in p; site-specific c	20	21.20	26.07
$p_{(T*s)}c_{(T*s)}$	site-specific time trends in p and c	25	21.51	23.74
$p_{(t*s)}c_{(t*s)}$	time and site-specific p and c	40	38.22	30.90

Table 3: Habitat-specific deer mouse population growth rates (over 30 days), calculated as the dominant eigenvalue of the projection matrix at stable age distribution. In each case, habitat-specific adult survival estimates from field data, were coupled with other demographic rates from the literature to project population growth rates (Appendix).

Habitat	Survival	Projected Growth Rate
Clearcut	0.87	1.17
Fragment Edge	0.78	1.03
Fragment Interior	0.77	1.00
Unfragmented (Control)	0.61	0.78

Table 4: Deer mouse density (SE) per 10,000 m^2 in August of 1998 and 1999 on all five study sites in southwestern Oregon.

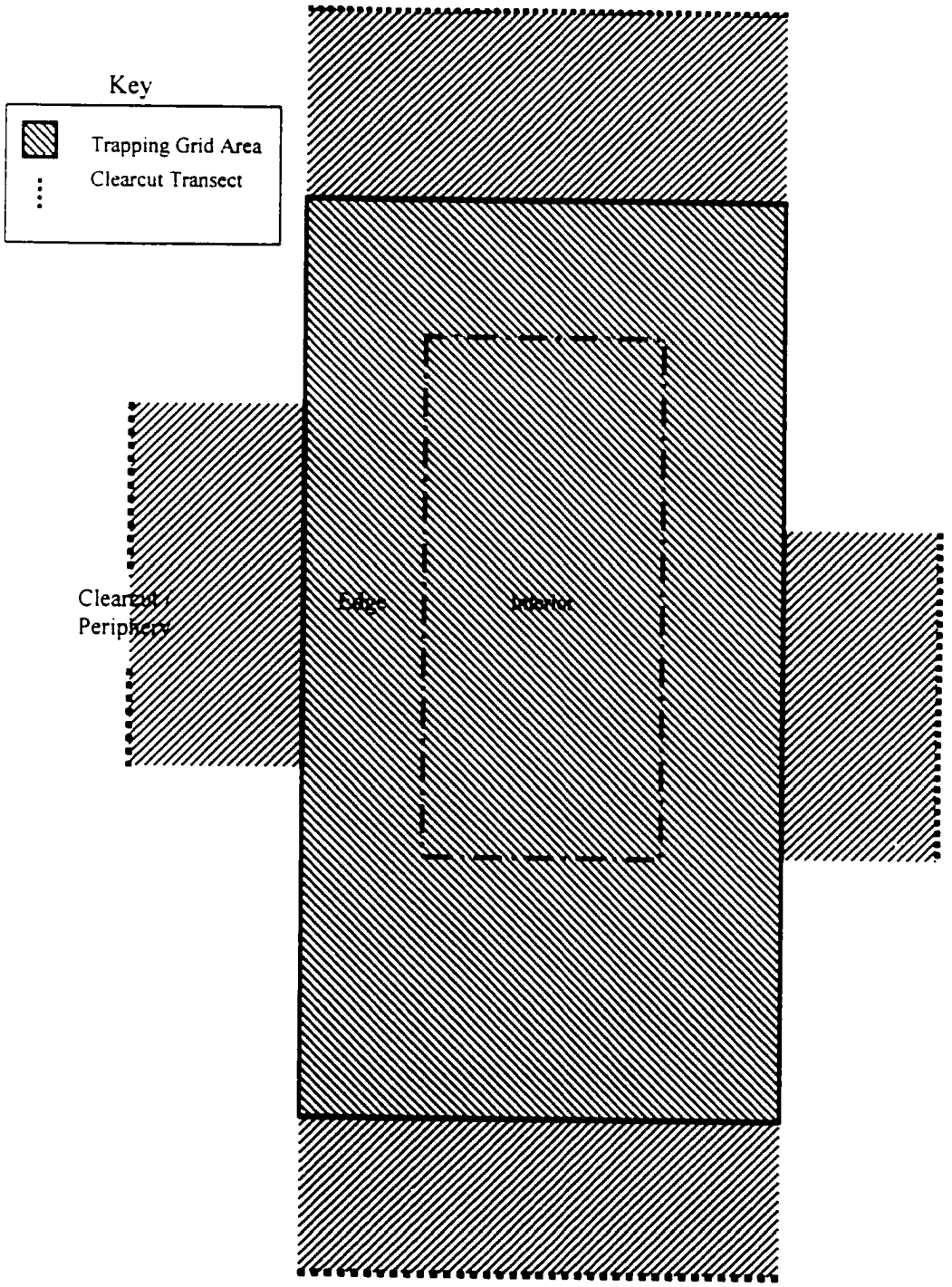
	Density	
Site	1998	1999
Fragments		
F1	7.20 (1.23)	6.66 (1.76)
F2	8.66 (1.63)	5.61 (1.40)
F3	13.63 (3.83)	8.08 (1.80)
Controls		
C1	0.35 (0.04)	0.62 (0.01)
C2	2.42 (0.60)	1.27 (0.33)

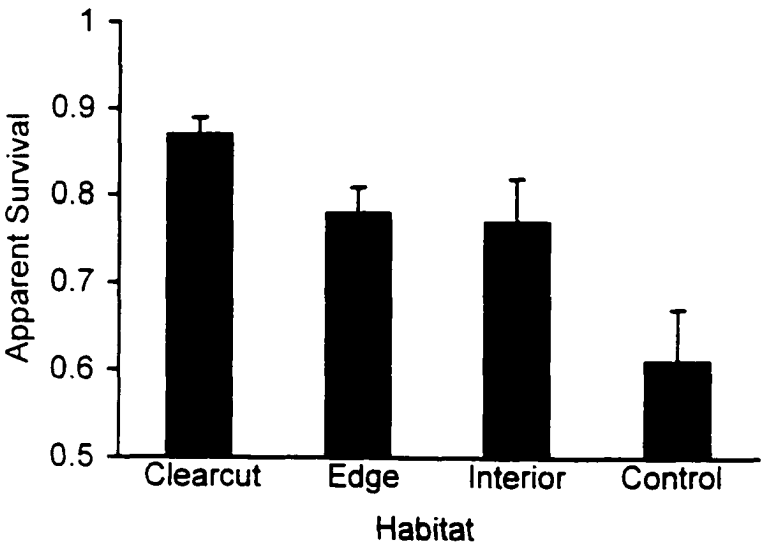
Figure 1: Trapping grid and peripheral transect design used to study small mammals on three forest fragments and two unfragmented control sites in southwest Oregon. Fragment sites differed in size and dimensions, but each was completely covered by a trapping grid. The shaded area was used in density calculations for each site. Each transect contained 6 traps spaced 15 m apart. Transects were placed in clearcuts surrounding fragment grids and in contiguous forest surrounding control grids.

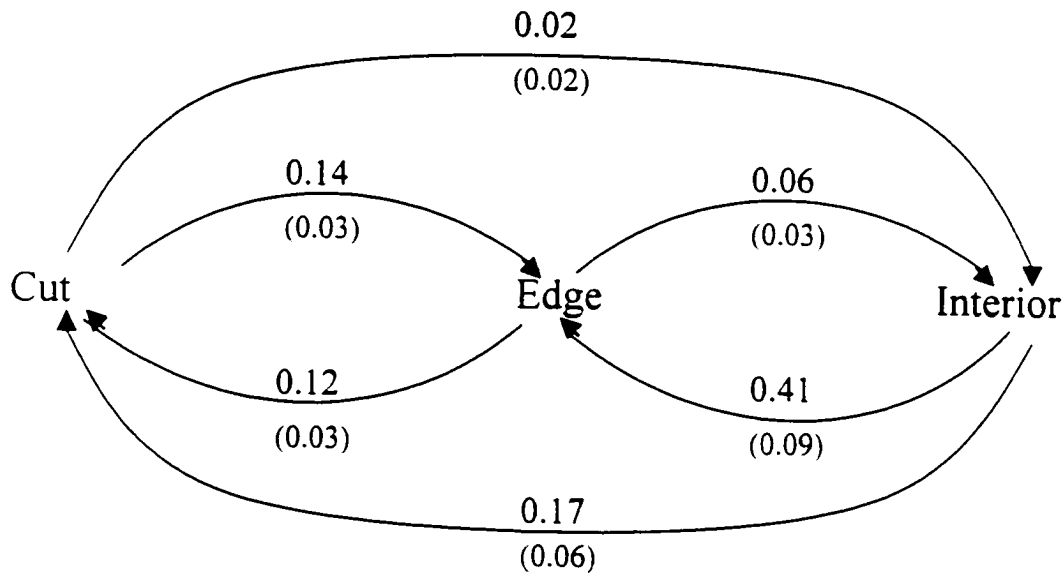
Figure 2: Habitat-specific deer mouse survival (and SE) estimates from three forest fragment sites and two unfragmented control sites in southwestern Oregon.

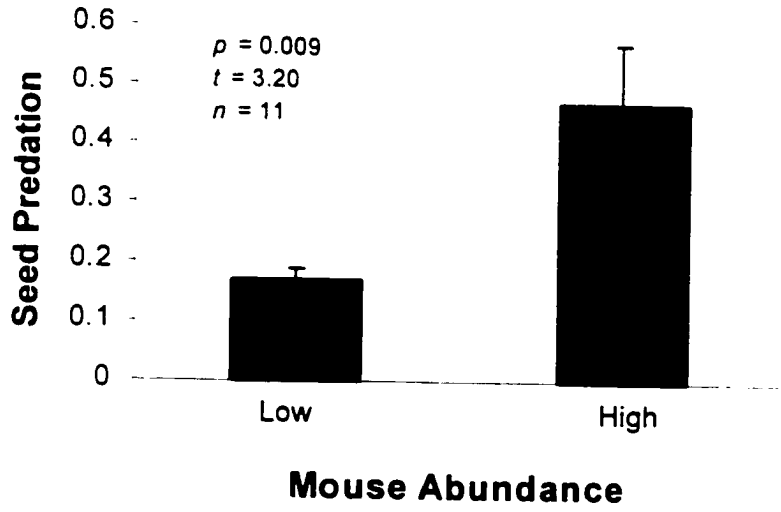
Figure 3: Deer mouse movement (and SE) estimates among clearcut, edge, and interior habitats at forest fragment sites in southwestern Oregon.

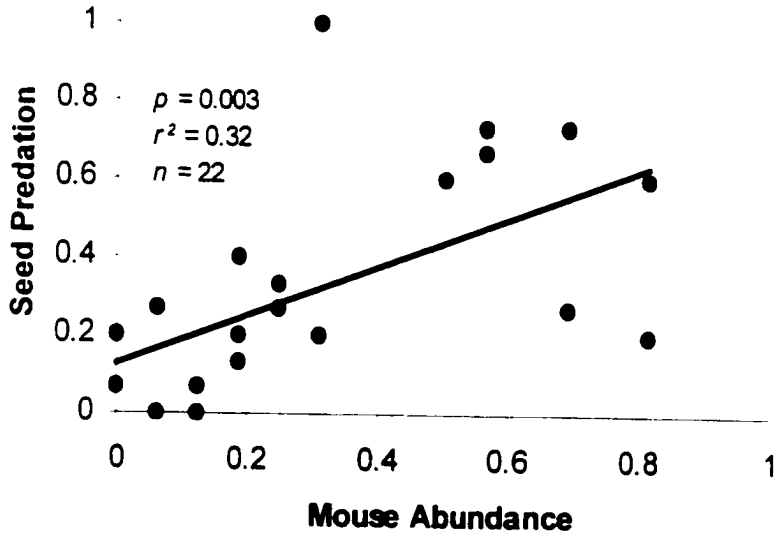
Figure 4: Trillium seed predation by deer mice. (a) The difference in proportion of trillium seeds predated at trap stations with the highest and lowest relative mouse abundances in each clearcut transect. (b) The effect of relative mouse abundance (# captures / # nights) on trillium seed predation across all trapping stations used in the seed trials.











Chapter 6 - Biology and Policy: Local Input in Salmon Conservation and Recovery

INTRODUCTION

The recent decline of Pacific salmon (*Oncorynchus spp.*) in the Northwest of the US has been well documented in the popular media. There also have been many scientific articles, books, and public debates concerning what should be done to curb the loss of salmon. The widespread and bitter debate over salmon conservation is ultimately due to complex life histories of salmon and how these life histories intersect with human economic activities. Salmon depend upon clean rivers for spawning, safe passage through fresh, brackish, and salt water to link their late and early life history stages, and adequate ocean conditions for growth and maturation. Consequently, there are multiple threats to all phases of their life cycle, often categorized under the four "H's" – habitat, hatcheries, hydropower, and harvest. These threats are well-documented, but still hugely controversial in terms of their relative importance to salmon conservation (Mann and Plummer 2000).

The National Marine Fisheries Service (NMFS) is at the center of all Pacific salmon conservation issues, because it is charged with salmon listing determinations under the Endangered Species Act (ESA). Any ESA listing determination, whether for or against listing under the ESA is likely to meet with sharp public criticism from at least one concerned party. Consequently, NMFS is constantly assaulted with lawsuits from all parties concerned with salmon conservation. Unfortunately, past efforts to conserve salmon have not met with success. None of the salmon listed

under the ESA has been de-listed and it is estimated that salmon are extinct from 40% of their original range (Anderson 1993).

As a result, different avenues to achieve salmon recovery have been proposed (*e.g.*, Lee 1993). Most recently, recovery efforts that incorporate greater local and regional input into ESA recovery planning have become popular. Below, I outline the ESA listing process and discuss the consequences of this shift toward greater local involvement to save salmon, by focusing on two case studies, Oregon coast coho (*O. kisutch*) and current recovery efforts in the Puget Sound region. In the case of the Oregon coast coho, the courts rebuffed NMFS in its attempt to avoid listing. I use Hood Canal summer chum (*O. keta*) and Lake Ozette sockeye (*O. nerka*) as examples to illustrate a potential problem with the policy shift NMFS has made toward increasing the participation of local groups and geographically-based recovery teams.

LISTING OF SALMON UNDER THE ESA

NMFS has developed a sound set of ESA listing procedures (Figure 1). The NMFS listing process is long and arduous, and includes data and input from many different parties. Primarily, it requires NMFS scientists to examine existing biological data to determine whether or not a given set of salmon population(s) is unique and faces a foreseeable risk of extinction. Then, after scientific conclusions are formed and conveyed by scientists to the NMFS Regional Office, the Regional Office makes public a determination of whether or not listing will occur.

Waples (1991) developed the NMFS criteria used to determine whether or not different salmon populations should be considered for listing, and ultimately receive

protection, under the ESA. The ESA provides for protection of distinct population segments. Consequently, an important facet of the NMFS criteria is the consideration given to genetic and ecological properties of a proposed population or group of populations, to determine whether or not it is an evolutionarily significant unit (ESU).

The listing process begins when NMFS convenes a Biological Review Team (BRT) to determine if a proposed population or set of populations is an ESU, based upon explicit and standardized information (Figure 1). If a population or set of populations is an ESU, each BRT is to consider several factors in making ESA listing recommendations. Specifically, the BRT considers the current and historic abundances, the spatial and temporal distribution of existing fish, population trends, factors posing demographic and genetic threats, and recent events with predictable short-term effects (Table 1; Wainwright and Kope 1999). After consideration of these factors, the BRT makes a recommendation to the regional NMFS office for listing an ESU and the regional office releases an official proposed status determination.

These ESA listing criteria are based on evolutionary and ecological considerations, so the salmon ESA listing process is scientifically sound, though sometimes based on qualitative information. And, although the listing process includes opportunities for public participation and comment on NMFS status determinations, as well as reviews from outside experts of conclusions reached by BRTs, the status recommendations are based upon "scientific information" (Waples 1995).

STATE INITIATIVES AND OREGON COAST COHO

Recently, controversy has swirled around the Oregon coast coho salmon ESU listing. The reasons for this controversy are manifold, but center around the consideration of new kinds of information by NMFS in its listing determination. In all previous listing determinations, NMFS had primarily relied upon existing biological data to determine whether or not any ESU should receive ESA protection. In 1995, NMFS proposed that the Oregon coast Coho was "likely to become endangered in the foreseeable future" and worthy of what is commonly called "threatened" status under the ESA. This proposal followed the scientific conclusions of the BRT based on an assessment of extinction risk facing this ESU (Weitkamp et al. 1995). The BRT had come to this conclusion based on reductions in the number of coho to roughly 5% of historic escapements, potential threats from hatchery fish to natural populations, and decreases in the number of recruits per spawner and pre-harvest numbers of fish (Table 1). The main uncertainties in the biological data cited by the BRT were the effects of hatchery strays on natural population trends, freshwater habitat conditions, and the effects of ocean conditions on natural populations.

Following the proposed listing of the Oregon coast coho as threatened under the ESA, some important factors changed (Figure 3). First, escapement in this ESU increased during the 1990's and the trends in these data became clearer after the 1995 proposed listing (Table 1). However, escapement was still only 10% of historic levels. In addition, the BRT considered three very different models used to analyze

the viability of this ESU (Table 1). These models predicted widely different outcomes for the ESU that varied from quite optimistic to drastic declines.

Perhaps more important than any observed changes in biological patterns or predictions for this ESU was the new policy approach NMFS undertook. This approach consisted of negotiations with the State of Oregon to avoid listing the Oregon coast coho ESU as threatened in its final determination (Figure 3). In order to avoid the federal regulations on take and critical habitat that follow "threatened" or "endangered" determinations, Oregon promised to immediately implement a wide range of conservation efforts to improve the status of coho, including unprecedented harvest restrictions, forestry and hatchery reforms, and efforts to restore freshwater habitats. These efforts (called The Plan here) were negotiated by the timber industry, private consultants, state, and federal agencies, and were to be undertaken by both private and state parties.

The NMFS Regional Office then asked the BRT to evaluate the status of the Oregon coast coho ESU with and without implementation of the hatchery and harvest parts of The Plan (Table 1). This marked a notable departure from previous status reviews because only the regional office had previously considered how promised conservation actions would affect an ESU. In this case, the BRT was asked to consider the effects of these actions. It is important to note that the BRT did not consider the likelihood that reforms would be funded and carried-out, only what the biological implications of these reforms would be, assuming that they were carried-out as stated (NMFS 1998b).

The BRT came to different conclusions based on the two scenarios considered. The BRT concluded that this ESU should receive "threatened" status given the existing data, though a few BRT members did not feel listing was necessary. After assuming the potential benefits of The Plan would be obtained in their second status review scenario, the BRT was "about evenly split" as to whether or not threatened status was still warranted (1997 Status Review). Although the BRT vote tally was not released in the Federal Register, later court cases revealed that seven members still favored threatened status, eight members favored "not warranted" status, and one member was undecided (RS Waples, *pers. comm.*).

In May, 1997, the NMFS Regional Office made a final rule listing in the Federal Register that the Oregon coast coho did not warrant listing as threatened under the ESA (NMFS 1997). This listing was preceded by a Memorandum of Agreement between the State of Oregon and NMFS, which promised implementation of The Plan by Oregon and a determination by NMFS that the Oregon coast coho ESU would not be listed as threatened. In addition, the Memorandum stated that NMFS could change this ESU's status to threatened if its condition deteriorated. Essentially, NMFS had decided to assume that The Plan would keep salmon from becoming endangered in the foreseeable future, even though the BRT was "roughly evenly split" as to whether or not the biological data and promises made by Oregon warranted this conclusion.

Subsequent lawsuits resulted in NMFS reversing this decision, because it was determined that NMFS could not rely upon future promises of improved conditions in its ESU listing decisions. Following these successful lawsuits, the Oregon Coast

coho ESU was listed as threatened in the Federal Register on August 10, 1998 (NMFS 1998b). Thereafter, proposed critical habitat and take regulations were issued, and following a public comment period, final critical habitat and take regulations were released (Figure 3). No recovery plan has yet been issued.

The Oregon coast coho listing process was important because it marked a departure from past status determinations that had relied upon existing biological data as the primary factors for decision-making. Instead, NMFS attempted to rely upon promised reforms as a means to recover an ESU that was, in exchange, to be officially recognized as not in need of the federal protections that accompany ESA listing. Whether or not the consideration of The Plan in listing determinations was a good idea is now a moot point. The courts have ruled that NMFS cannot use promises from state or private parties in ESU listing determinations, and this ESU is listed as threatened under the ESA.

It is interesting to consider whether or not the promises made by non-Federal parties to avoid listing of the Oregon coast coho ESU would have improved this ESU's status. Although federal regulations are now in effect as a result of the threatened determination, it would be worthwhile to partition out the contributions of the proposed local and regional reforms to recovery. NMFS committed itself to working with non-Federal parties involved in The Plan to recover this ESU despite the court ruling (NMFS 1998b). In turn, some of these parties have promised to work with NMFS toward recovery, even though the ESU has been listed. The forestry reforms that will be undertaken despite the listing include large-scale efforts by private companies and state foresters to avoid further harm to coho habitat, as well as

efforts to improve existing degraded habitat. In addition, some of the promised hatchery reforms have been attempted. Unfortunately, it will take time to see whether or not recovery will meet with success under federal regulations. And, it will be impossible to truly tease apart the contribution that local and regional initiatives will make to coho recovery, because federal regulations and restrictions have overshadowed them.

LOCAL INPUT ON RECOVERY PLANS FOR THE PUGET SOUND

Recovery planning differs from ESA listing determinations in important ways. The ESA requires that Recovery Plans include (1) objective, measurable goals for delisting; (2) a comprehensive list of the actions necessary to achieve the delisting goals; and (3) an estimate of the cost and time required to carry out those actions. Most importantly, recovery plans are not limited to biological data. They incorporate considerations of habitat needs, regulatory needs, and economic costs of recovery. The essential role of recovery plans is to determine what factors must be changed or addressed in order to improve the status of an ESU to the point where protection under the ESA is no longer necessary.

NMFS has divided recovery planning into two "phases" (NMFS 2000). Phase I involves the identification of "delisting criteria" which should be met in order to eliminate the risk of extinction. This is regarded by NMFS as primarily the responsibility of scientists. Phase II includes a consideration of economic and social impacts of recovery, as well as the needs of the ESU identified by scientists, and is regarded by NMFS as mostly a policy exercise.

Due, in part, to frustrations surrounding the listing and recovery of ESUs, NMFS has embarked on a new approach to the development of recovery plans. In several different press releases, NMFS has announced that local input will be an important component of recovery planning (*e.g.*, NMFS 2000). This emphasis on local input in natural resource planning has recently gained attention as an improved means to resolve contentious public issues (Kemmis 1990).

The new recovery planning structure includes local and regional groups overseen by a Recovery Science Review Panel (RSRP) appointed by NMFS (Figure 4). The RSRP is charged with reviewing core principles and elements of the recovery planning process, ensuring that well-accepted and consistent ecological and evolutionary principles form the basis for all recovery efforts, reviewing processes and products of all Technical Recovery Teams (described below) for scientific credibility and consistency, and overseeing peer review for all recovery plans and products (NMFS 1999). It is important to note a few things about the RSRP. None of the recovery plans will actually be written or approved by the RSRP. The RSRP consists entirely of academics that have made significant contributions to the study of evolution and ecology, but none is a salmon biologist. The primary purpose of the RSRP is to serve as a source of ecological and evolutionary insights into recovery planning.

Beneath the RSRP are the groups that are charged with determining delisting criteria for each ESU -- regional Technical Recovery Teams (TRTs). Although a NMFS science center researcher chairs each TRT, the TRT members have diverse employers. The Puget Sound TRT, which oversees the region including Lake Ozette

Sockeye and Hood Canal summer chum, is composed of representatives from many different agencies and interest groups, including county, state and federal agencies, and tribal organizations (Figure 4).

NMFS has also encouraged interactions between each TRT and interested "third parties". In the Puget Sound there are two organized third parties in the form of committees that have proposed recovery activities (Figure 4). Various actions proposed by these third parties have been adopted as interim recovery plans until official recovery plans are written. Unfortunately, NMFS has not identified who will write official recovery plans, so it is unclear how much influence locally organized committees and other third parties will have on recovery planning. In publicly available documents NMFS has stated, somewhat confusingly "TRTs will identify recovery goals for all listed ESUs. Although the TRTs will not identify formal recovery goals for candidate species, they will identify factors of concern and measures to ensure the long-term conservation of such species" and suggest interim recovery activities until formal recovery plans are drafted (NMFS 2000). However, exactly who will identify formal recovery plans is not explicitly stated by NMFS. To date, all available documents proposed for recovery actions in this region have been written by locally based committees devoted to summer chum recovery (Ames et al. 2000) and Ozette sockeye (Makah Tribal Fisheries 2000).

The existing third party committees include representatives from local counties, timber companies, tribes, and federal and state agencies. These committees reflect NMFS' commitment to work with the state, local, tribal, and private parties "to develop recovery plans that are appropriate to each region" (NMFS 2000). In the

case of the Ozette sockeye, the current committee includes representatives of most of the landowners surrounding Lake Ozette, including four timber companies, two Indian tribes, various federal and stage agencies, and Clallam County (Figure 4). The Hood Canal summer chum committee has representatives from a similar set of groups.

Although local support is important for recovery plans to succeed, it appears that NMFS is facing an inherent conflict in perspective between the different levels involved in recovery planning. The RSRP consists of ecologists and evolutionary biologists, who are likely to exert a top-down pressure for a greater evolutionary and ecological perspective than has traditionally been incorporated into fisheries biology (Bottom 1999). In contrast, the TRTs and committees that advise them consist mostly of fisheries biologists, who traditionally receive a very different education and have a different philosophy that has its roots deep in the last century (McIntosh 1985). As an example, many of the fisheries biologists currently on the TRT and local committees are representatives of parties that have historically been strong proponents of the use of fish hatcheries for salmon mitigation and recovery.

The only existing recovery planning documents for Hood Canal summer chum and Ozette sockeye support extensive use of hatcheries as recovery tools. The proposed recovery plan developed by the Hood Canal summer chum committee (Ames et al. 2000) gives a disproportionately large role to hatcheries rather than habitat improvement or forestry and harvest reforms. The interim recovery plans now being used for Ozette sockeye recovery also emphasize the role of the Lake Ozette hatchery population in recovery efforts (Makah Tribal Fisheries 2000). This is

despite the fact that the hatchery populations of chum and sockeye, though included in both ESUs, have been deemed to be "non-essential" for recovery of the naturally spawning populations (NMFS 1998a, 1998b).

There is sound evolutionary justification for minimizing the role of hatcheries in recovery planning for naturally spawning salmon populations that are "essential" for meeting de-listing criteria. Most of the existing evidence suggests that although hatcheries are not inherently bad (Waples 1999), they usually contribute to the decline of naturally spawning salmon populations through competition and hybridization (*e.g.*, Allendorf and Ryman 1987, Reisenbichler and McIntyre 1977). In other words, hatchery fish have generally lowered the fitness of naturally spawned ones (for other examples see Ford and Hard 2000). In addition, because hatcheries are expensive and will compete with habitat improvement efforts for available recovery funds, there are other reasons for minimizing any reliance on hatcheries in recovery planning (Meffe 1992, Lichatowich et al. 1999).

A sound evolutionary or ecological interpretation of the existing literature suggests that hatcheries are unlikely to improve the health of the naturally spawning populations that compose the "essential" portions of these ESUs. Thus, there seems little reason to doubt that the top-down pressure from the RSRP, which oversees all efforts of the regional TRTs, will reject a hatchery-based approach to recovery. Existing evidence suggests that that components of the recovery plans developed by locally based groups will continue feature hatchery programs in recovery planning. Consequently, there will be tension between the hatchery dependence of recovery

plans developed at the local and regional levels and the evolutionary/ecological perspective that will likely be espoused by the RSRP.

It seems likely that the reliance on hatcheries as interim recovery tools will increase the prominence of hatcheries in official recovery plans. That is, once hatchery programs are given approval as prominent components of short-term recovery planning (as they have for Ozette Sockeye), this increases likelihood that they will become components of the recovery plans ultimately used for long-term recovery planning.

The differences between an evolutionary perspective and a traditional fisheries biology perspective may lead to greater acrimony between the different levels of the recovery planning hierarchy than differences dictated by the geographic location of the groups involved. The primary reason salmon recovery is likely to falter is not the "heavy-handedness" of federal restrictions or a lack of local involvement. Rather, a greater threat is the lack of an evolutionary perspective being incorporated into recovery planning at all geographic and bureaucratic levels. That is, RSRP members should be included in planning on the local, regional, and larger scales. Until this occurs, it seems likely that existing efforts at recovery will continue to be mired in conflict and failure based upon faulty assumptions about failed technologies.

CONCLUSIONS

NMFS uses a very sound decision-making process for determining the status of "species" proposed for listing under the ESA. The strength of the criteria used by

NMFS for listing is that they rely upon genetic and ecological data for answers (Waples 1995). NMFS has recently attempted to incorporate greater local and regional input into listing and recovery efforts for Pacific salmon, due in part to a lack of past success in recovering salmon and the popularity of the "local" approach to natural resource conservation.

In the case of Oregon coast coho, an attempt to avoid federal listing of this ESU as threatened in exchange for promised statewide reforms was rejected by the courts as illegal. It is too early to tell whether the promised reforms, which have been implemented to some degree despite the courts' rejection of The Plan, will have enough of an impact on this ESU to remove it from the threatened list.

The new recovery planning hierarchy NMFS has developed will create a tension between local recovery committees and regional TRTs that consist mostly of fisheries biologists and the RSRP. It seems likely, given the evolutionary background of the RSRP and the preponderance of existing data, that the RSRP will not give "scientific approval" to recovery plans that emphasize hatcheries in recovery. As a result, the development of recovery plans may be slowed by a conflict in thinking between traditional fisheries biology and evolutionary ecology (Lichatowich et al.1999), while ESUs continue to decline. If locally developed plans continue rely upon hatcheries for recovery and these plans are incorporated into final recovery plans, existing studies suggest recovery of essential populations will be hampered. If locally and regionally developed plans used in interim recovery activities are not incorporated into final recovery plans, it may engender even greater local resentment of federal actions than now exists. A more sound approach might be to ensure that an

evolutionary perspective is incorporated into all phases of recovery planning. This would ensure a sound recovery program and minimize local resentment of federal rules and regulations.

Table 1: Criteria used and conclusions made by NMFS Oregon Coast coho Biological Recovery Team. Included are findings in 1995 Status Review and 1997 Status Review Update, which included evaluation of status without, and with (+ The Plan) consideration of proposed conservation actions by the State of Oregon.

Factor Considered	1995 Status	1997 Status	1997 Status + The Plan
Abundance and Spatial/ Temporal Distribution	↓ Abundance	45 K spawners (slight ↑ over '95)	↑ # spawners
Current vs. Historic Abundance and "K"	< 5% escapement of early 1900's	ocean run is 72K (< 10% early 1900's)	N/A
Trends in Abundance	constant spawner abundance since 70's pre-harvest # ↓ avg. recruits/spawner ↓	escapement ↑ in 90's recruitment still ↓	N/A
Causes of Variation in Abundance and Survival		maybe freshwater production or ocean conditions	would ↓ harvest; but this might be weakened in 2000

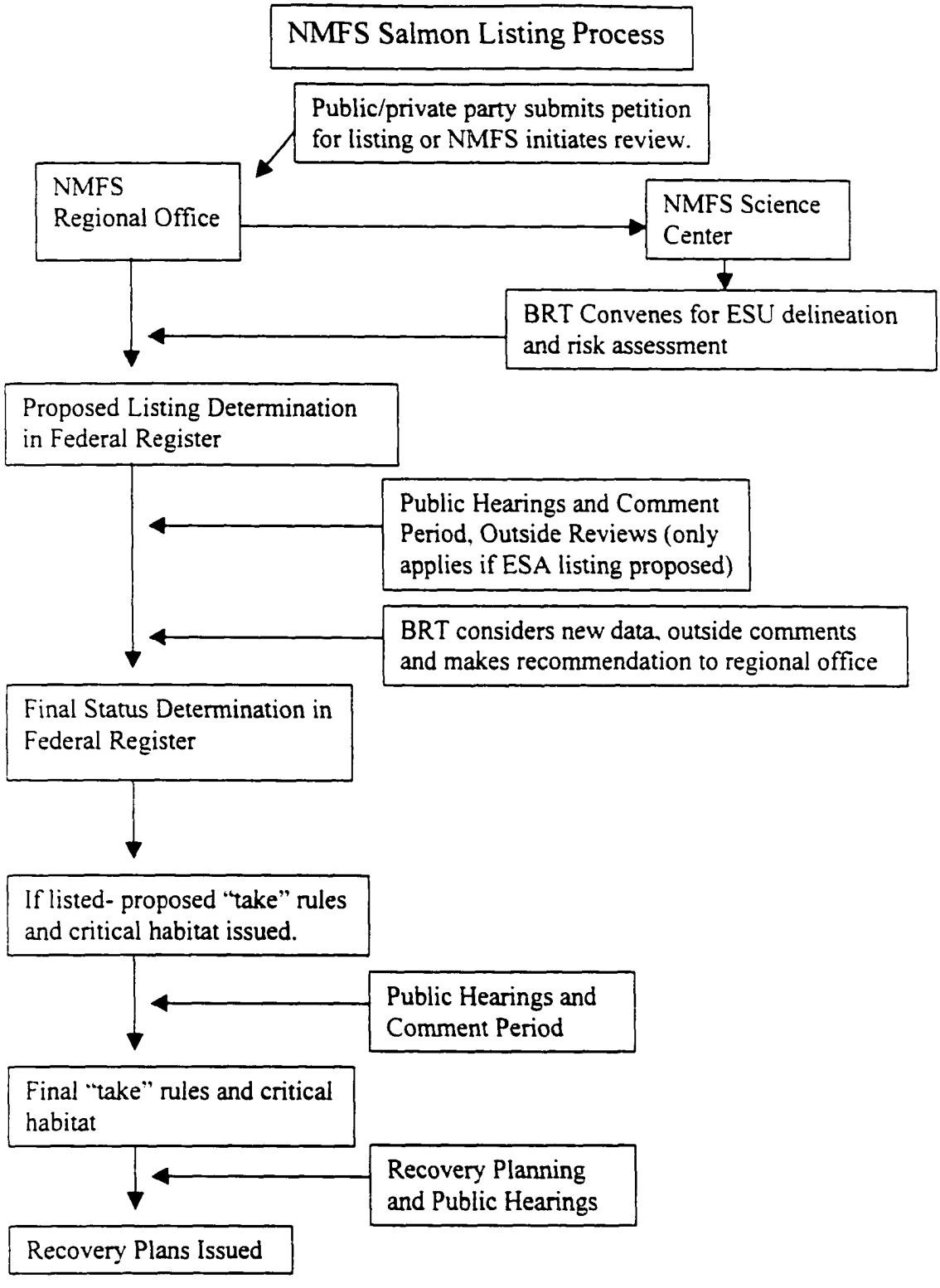
Factor Considered	1995 Status	1997 Status	1997 Status + Plan
Threats to Genetic Integrity	heavy hatchery influence in most major rivers	tentative evidence of ↓ hatchery strays	↓ hatchery threat; some probs. will remain
Recent Events w/ Short Term Effects		'96 floods— ↓ juv. fish survival some areas	N/A
BRT Conclusion	**threatened**	**threatened, some BRT members disagree**	**BRT evenly split on threatened status**
Main Uncertainties	extent of hatchery straying, hatchery influence on natural population trends, condition of freshwater habitat, ocean condition effects	hatchery straying effects, habitat quality changes	hatchery straying effects, long-term harvest restrictions, habitat quality

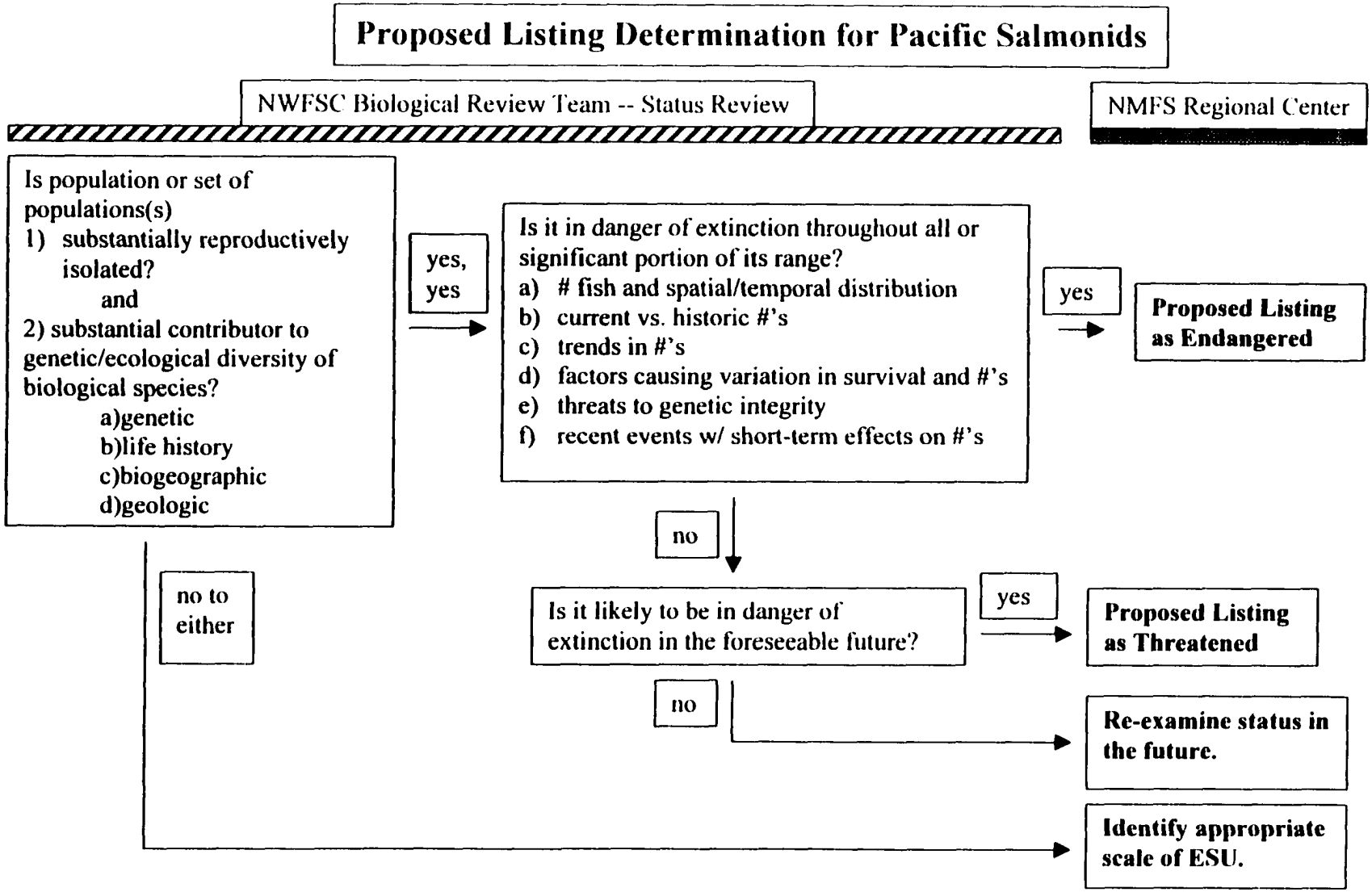
Figure 1: The steps used by the National Marine Fisheries Service to protect salmon under the Endangered Species Act.

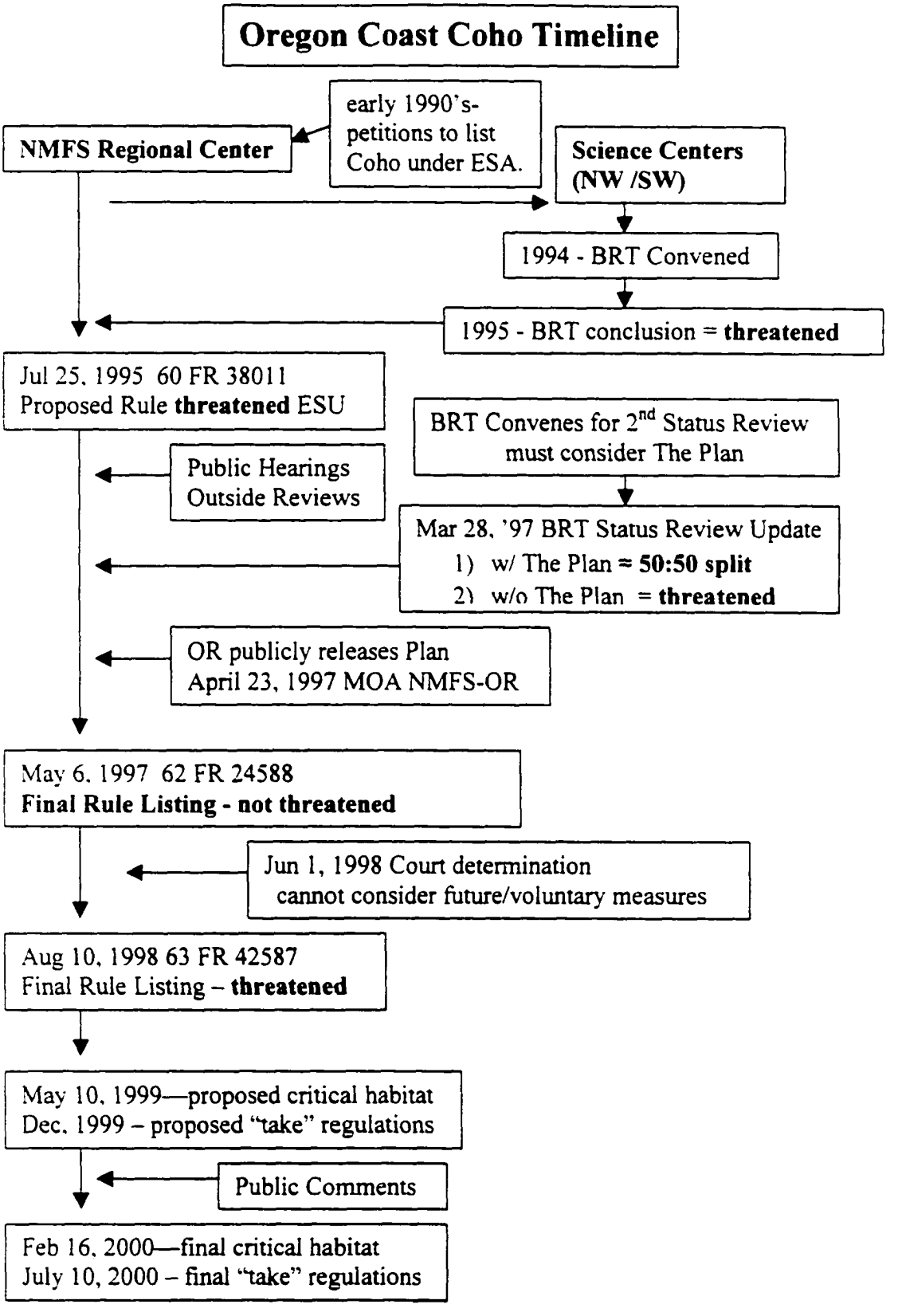
Figure 2: The criteria used to determine whether proposed populations of salmon are Evolutionarily Significant Units that warrant protection under the Endangered Species Act.

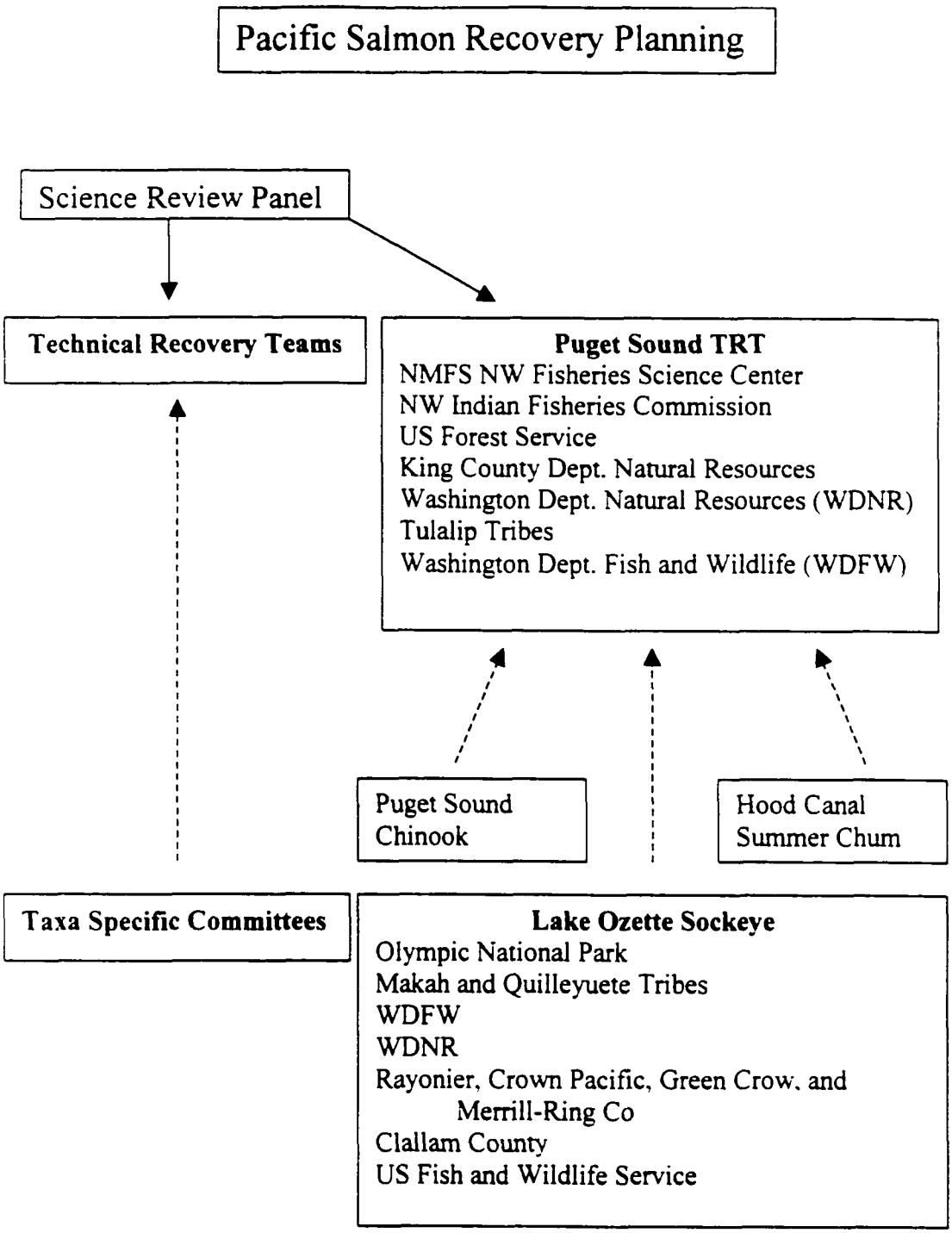
Figure 3: The history of the listing process for the Oregon coast coho.

Figure 4: The current hierarchy used by the National Marine Fisheries Service to develop recovery plans for salmon listed under the Endangered Species Act. The right side of the figure shows the parties represented on the Puget Sound Technical Recovery Team and the Lake Ozette sockeye committee.









Appendix 1: Descriptions, numbers of parameters, and ΔAIC values[a] of models used to estimate vole abundances at four sites in each of eight trapping sessions. Models included different combinations of variation in capture probabilites (p) and recapture probabilites (c). Values in bold print are the number of parameters and ΔAIC values for the best-supported model in each session. Also shown are p and c estimates for each trapping session.

		1998				1999			
Model	Description	1	2	3	4	1	2	3	4
$p_{(.)}c_{(.)}$	constant p and c	6	6	6	6	6	6	6	**6**
		19.24	15.94	5.57	4.57	3.55	5.92	1.41	**0.00**
$p_{(T)}c_{(.)}$	linear time trend in p; constant c	7	7	7	7	7	**7**	**7**	7
		0.34	11.47	4.09	1.88	0.99	**0.00**	**0.00**	2.00
$p_{(T)}c_{(T)}$	linear time trends in p & c	**8**	8	8	8	8	8	8	8
		0.00	3.99	4.58	1.16	3.12	2.00	2.01	3.75
$p_{(t)}c_{(.)}$	time dependent p; constant c	13	9	**9**	**9**	**9**	9	9	9
		0.29	2.49	**0.00**	**0.00**	**0.00**	0.17	1.41	3.45

Model	Description	1998				1999			
		1	2	3	4	1	2	3	4
$p_{(t)}c_{(t)}$	time dependent p & c	19	**11**	11	11	11	11	11	11
		2.94	**0.00**	2.45	1.34	4.08	4.35	5.51	7.01
$p_{(t)}c_{(s*t)}$	time dependent p; site by time dependent c	40	20	20	20	20	20	20	20
		27.22	10.03	15.07	7.30	11.15	12.40	20.39	11.03
$p_{(s+T)}c_{(s+T)}$	site and time trend effects on p and c	14	14	14	14	14	14	14	14
		1.95	9.64	12.62	7.23	4.77	8.17	6.85	9.91
$p_{(s*T)}c_{(s*t)}$	site by time trend effects on p; site by time	40	24	24	24	24	24	24	24
	effects on c	25.01	28.27	27.41	16.17	23.37	22.77	25.66	20.99
$p_{(s*t)}c_{(s)}$	site by time effects on p and site effects on c	40	24	24	24	24	24	24	24
		21.82	22.03	22.39	10.84	18.08	23.16	18.89	26.61
$p_{(s*t)}c_{(s*t)}$	site by time effects on p and c	60	32	32	32	32	32	32	32
		54.03	28.29	23.51	16.19	35.16	35.84	36.32	34.15

p estimate for trapping session	0.92	1.00	1.00	1.00	1.00	0.98	0.99	0.99
c estimate for trapping session	0.96	0.89	0.96	0.98	0.94	0.87	0.87	0.93

[a] ΔAIC is the difference in AIC values between a given model and the one that provides the best fit to the data. Therefore ΔAIC is always zero for the best model.

Appendix 2: Polymerase chain reaction reactants and annealing temperature used to amplify the mtDNA control region and five microsatellite loci in California red-backed voles. All concentrations are millimoles except where noted. Also shown are the number of alleles detected.

		Locus				
	mtDNA	*CRB-5*	*CRB-6*	*Cgl-4*	*Cgl-15*	*Cgl-19*
Tris-HCl (pH 8.3)	10	10	10	10	10	10
KCl	50	50	50	50	50	50
$MgCl_2$	2.0	1.2	1.0	1.0	1.1	1.2
each dNTP	0.25	0.25	0.25	0.25	0.25	0.25
each primer	10	10	10	10	10	15
Perkin-Elmer Taq (units)	2.0	0.5	0.5	0.5	0.5	0.5
Flouresceine label	-	HEX	FAM	HEX	HEX	HEX
Annealing Temp (°C)	55	59	52	59	52	52
total # alleles detected	5	17	15	17	13	14

Appendix 3: Stage-based matrix projection model used to examine how differences in adult survival across habitats influence population growth rate. Adult survival was estimated in this study and ranges from 0.61 to 0.87 across different habitats. Other vital rates are mean values for female life stages from other studies conducted in the Pacific Northwest. All vital rates were adjusted to a 30 d projection interval. Population growth rates are the dominant eigenvalue of the projection matrix at stable age distribution.

Projection Matrix

0	0	(2.59)(0.60)(A)
0.48	0	0
0	A	A

Matrix Values

0.48 = survival of pre-trappable mice (Sullivan (1979), Van Horne (1981)).

A = adult survival (Figure 2).

2.59 = number of female offspring/litter (Sheppe (1963), Van Horne (1981)).

0.60 = proportion of adults breeding (Sullivan (1979), Sullivan and Sullivan (1981)).

Appendix 4: Fragmentation Affects Nest Predation in a Historically Fragmented Western Coniferous Forest

Abstract

Forest fragmentation can have dramatic influences on the demography of birds; however, effects are variable and sometimes unclear, particularly in historically (naturally) fragmented forests. We investigated predation rates on artificial nests in fragmented versus unfragmented forests within a historically fragmented coniferous forest ecosystem in southwestern Oregon, USA. Predation rates were higher on nests in forest fragments surrounded by clearcuts than in continuous forest. Higher predation in fragments was found on artificial nests in all four distinct microclimates that mimicked real nest sites of important passerine species within the community. While predation by small mammals was consistent across fragmented and unfragmented sites, predation by birds and large mammals was higher on fragmented sites. Overall, these results contrast with hypotheses that increases in nest predation are unlikely when fragmentation occurs through timber harvest, or when it occurs in forests that were historically naturally fragmented. Our study suggests that increased predation rates on fragments were caused by predators that were larger than those on the unfragmented sites. The management implications of our results are amplified by the large proportion of forests in the western U.S. that have been fragmented by timber harvest.

Introduction

The impact of habitat fragmentation on bird populations is a major issue in avian conservation. Since 1984, at least 47 published studies have tested the effects of forest fragmentation on nest predation (reviewed by Marzluff and Restani 1999), and many have shown that fragmentation can lead to increased rates of nest predation. Some studies have found "edge effects", in which predation is elevated near forest edges (Gates and Geysel 1978, Andren and Angelstam 1988, Robinson and Wilcove 1994, King et al. 1998). Others have shown that predation increases as fragment size decreases (Wilcove 1985, Møller 1988, Small and Hunter 1988, Hoover et al. 1995), or as the overall amount of fragmentation within a landscape increases (Yahner and Scott 1988, Robinson 1992, Robinson et al. 1995, Donovan et al. 1997). Because nest predation may be the most important determinant of breeding success, any increase in predation rates on forest birds in fragmented landscapes may have large demographic consequences that influence broad scale population stability (Ricklefs 1969, Martin 1992, Donovan et al. 1995).

As the body of literature examining the effects of forest fragmentation on bird populations has grown, it has become clear that increased rates of predation are not universal consequences of fragmentation. The negative effects detected in some parts of North America and Europe do not hold in other regions of both continents (Haila et al. 1989, Nour et al 1993, Rudnicky and Hunter 1993, Hanski et al. 1996, Huhta et al 1998). It appears that negative effects are dependent upon a number of factors, including the landscape type, predator community, history of disturbance within a region, and proportion of intact habitat remaining (Andren 1995, Vander Haegen and DeGraaf 1996, Tewksbury et al. 1998, Zanette and Jenkins 2000). Evidence suggests forest birds are

likely to be adversely affected when the matrix around remaining forest is agricultural or urban, perhaps due to increases in generalist predators associated with human habitation (Saunders 1990; Andren 1992, 1995; Bayne and Hobson 1997).

In contrast, studies in areas where mature forest stands lie within a matrix of younger, regenerating forest generally have failed to find evidence of negative fragmentation effects (Andren 1995). Negative effects are thought to be unlikely in timber-harvested forests (Yahner and Wright 1985, Ratti and Reese 1988, Rudnicky and Hunter 1993, Vander Haegen and DeGraaf 1996), partly because regenerating forests are unlikely to support high densities of nest predators (DeGraaf 1995, Hanski et al. 1996). Furthermore, the lack of negative fragmentation effects in some regions is thought to be linked to the natural heterogeneity of the landscape (Rudnicky and Hunter 1993, Schieck et al. 1995, Tewksbury et al. 1998, Marzluff and Restani 1999). For example, birds that breed in forests historically fragmented by natural processes (e.g., fire, wind, disease), may have evolved adaptations to disturbance, making them unlikely to suffer decreased breeding productivity in fragmented habitats (Bayne and Hobson 1997, Bock 1997, Schmiegelow et al 1997, Cotterill and Hannon 1999, Sallabanks et al. 1999).

If there are differences between fragmentation effects in agricultural/urban landscapes and forested or naturally heterogeneous landscapes, then this has important ecological and economic implications. In the Pacific Northwest, only 13-18% of prelogging old-growth forest remains (Booth 1991), and most remnant forest fragments in the western U.S. lie within a matrix of regenerating clearcuts, and not agricultural or urban habitat. These forests were historically fragmented by fires and other natural disturbances (Garman et al. 1999). If nest predation is not elevated in these remnant

patches, then forest-nesting birds may be relatively unaffected by forest fragmentation in these areas, and research and conservation dollars would be better spent on other taxa. However, if nest predation is elevated within forest fragments, then the sheer level of fragmentation that has occurred in coniferous forests is reason for concern and warrants increased management and research attention.

To address the question of whether or not forest fragmentation through timber harvest may lead to increased nest predation in a western coniferous forest, and to address possible underlying mechanisms of these effects, we conducted a field study using artificial nests. Specifically, we measured predation rates on artificial nests in a fragmented coniferous forest of southwestern Oregon historically subject to high rates of disturbance (Agee 1991, Taylor and Skinner 1998). We asked whether or not nests in forest fragments surrounded by clearcuts were more likely to be depredated than nests in continuous forests. We then investigated possible mechanisms affecting predation rates by examining predation rates relative to proximity to habitat edge and nest microhabitat. Finally, we compare the predator classes responsible for predation in fragment and unfragmented sites.

Methods

Study Area and Sites

Study sites were located in forests dominated by Douglas-fir (*Pseudostuga menziesii*) overstories and herbaceous understories in the Klamath Geological Province of southwestern Oregon (Franklin and Dyrness 1973). The southern research sites were located in the Sucker Creek drainage, which had an average fire return interval of 37

years prior to 1921 (Agee 1991). The fire histories of our northern sites, in the Mule and Cow Creek drainages, have not been detailed, but vegetation communities suggest the fire return intervals are likely to be similar but slightly longer than those recorded for the southern sites (Atzet and Wheeler 1982). The cycle of fire disturbance in southwestern Oregon historically created a complex mosaic of large forest stands of varying sizes and in various stages of regeneration (Agee 1991, Taylor and Skinner 1998). In the 20th century, fire suppression and timber harvest have changed this landscape into what is today a younger forest on average, with small fragments of remaining old-growth embedded in a matrix of clearcuts and regenerating forest (Jules 1998).

Within this fragmented landscape, we examined nest predation in 6 small forest fragments and 4 sites in "unfragmented" forests. Unfragmented forests were approximately 250-1000 ha of continuous forest, with our study sites at least 75 m from any forest edge, trail, or road. The 6 forest fragments were 0.9 ha – 6.5 ha of late succession forest completely surrounded by clearcuts. To reduce bias created by geographic variation, sites were matched such that each fragment was within 13 km of an unfragmented site. The limited number of forest stands within the study area >250 ha dictated that 2 of the unfragmented sites were matched with more than 1 fragment (Table 1). These sites have been used previously by Mills (1995, 1996) and Jules (1998), to investigate ecological effects of forest fragmentation.

Artificial nests

We studied nest predation rates by using artificial wicker nests approximately 11 cm diameter x 6 cm deep (Darice, Inc., Strongsville, OH). In each nest we placed 1 fresh

Japanese quail egg (*Coturnix coturnix*). In addition, 1 plasticine egg was painted to resemble a quail egg and wired to the nest. We washed the quail eggs in distilled water, wore latex gloves while handling nests and nest contents, and wore rubber boots on the study sites in order to minimize any human scent that might affect predation rates (Sieving 1992, Warner 2000). We also aired nests out in the forest for at least 3 days prior to use to reduce any unnatural scents.

We covered each site with a grid of nests, with 30 m spacing between adjacent nests. Fragments were saturated with as many nests as could fit within the site while maintaining the regular grid spacing. This approach kept the density of nests equal across all sites. The number of nests on each unfragmented site was roughly equal (within 4 nests) to the sum of the nests on the fragment(s) geographically matched with that unfragmented site.

We placed each nest in 1 of 4 microhabitats, in order to approximate the nest-microhabitats of 4 of the most important understory-nesting species found on our study sites: dark-eyed junco (*Junco hyemalis*), Pacific-slope flycatcher (*Empidonax difficilis*), Townsend's solitaire (*Myadestes townsendi*), and winter wren (*Troglodytes troglodytes*) (Ehrlich et al. 1986, Ralph et al. 1991) (Appendix A). Microhabitats were used in equal proportions on each site. The use of nest microhabitats was intended to reduce 3 types of potential bias: 1) differences in nest placement among study sites, 2) differences in locations between real nests and artificial nests (Major and Kendal 1996), and 3) density-dependent predation, which can occur when predators form a search image of nests within a single microhabitat (Martin 1988). Nests were placed 5-10 m from flags

marking the 30 m grid, and a small bit of flagging tape was placed under each one to identify its original position if moved by predators.

We set nests out in 4 trials between 11 June and 23 July, 1998 (Table 1), a period coinciding with much of the breeding season in our study area during this El Niño year (K. Jones, personal observation). Each trial consisted of a 14-day period in which nests were left unchecked on an unfragmented site and its geographically matched fragment(s). This period mimicks the natural incubation/laying period for eggs of our focal species. At the end of each trial, nests were recorded as depredated if either egg was removed from the nest, the real egg was cracked, or the plasticine egg showed clear tooth, claw, or beak marks. We identified predators by comparing teeth and beak marks left on the plasticine eggs to those made by museum specimens. We classified predation events into 1 of 6 categories which described the predator class and size relative to other predators on our study sites: a) small mammal (mouse, vole, or shrew), b) medium mammal (chipmunk or squirrel), c) large mammal (bobcat or larger), c) small bird (smaller than a jay), d) large bird (jay or larger), or e) unknown.

Statistical Analysis

There are 2 fundamentally different ways to analyze data in a study of effects of fragmentation and edge on nest predation. One approach is to treat the sites as the unit of replication, comparing predation levels on the N = 6 fragmented sites to that on the N = 4 unfragmented sites. Although statistically preferable, this approach suffers from the inevitable confound between fragment size and number of subsamples in interior edge classes. In other words, smaller fragments will have little to no area in the more interior

edge classes, so that probability of predation in certain edge classes are based on < 4 nests for several edge classes in several remnants.

Therefore, in addition to analyzing our data with the site as the unit of replication, we analyzed them using the nest as the experimental unit, comparing predation rates for the 148 nests on fragments to that of the 147 nests on unfragmented sites. Although this approach represents pseudoreplication, it has the advantage of increased power and of not suffering from the problem of geometry that leads to average nest predation being calculated based on very few nests on small fragments.

We used a Mann-Whitney *U*-test to evaluate whether predation rate on the 6 fragments differed from that on the 4 unfragmented sites. To test the same hypothesis at the level of individual nests, we used a 2 x 2 *G*-test (with William's correction) of nests depredated and not depredated on fragments and unfragmented sites (Sokal and Rohlf 1995). These same tests were used to evaluate differences in predation rate between fragmented and unfragmented sites for each of 4 nest microhabitats.

Finally, we evaluated the effect of proximity to the fragment edge and nest microhabitat (described above) on nest fate. Following Mills (1995), nests were classified into 1 of 4 edge classes according to distance from the fragment edge: < 15 m = 1, 16-30 m = 2 , 31-45 m = 3, and > 45 m = 4. Then, we then ran a logistic regression in SPSS version 8.0, using block entry to predict nest fate with the independent variables edge class and microhabitat.

Results

Of 295 nests in our study, 91 (30.8%) were depredated. Individual eggs were depredated at rates of 28.8% (85 of 295) for plasticine eggs, and 18.3% (54 of 295) for quail eggs. We identified predator group for 68 of the 91 predation events, but could not assign a predator class for 14 nests that had missing plasticine eggs and for 9 nests with inconclusive or no marks on the plasticine egg. Three of the original 298 nests were omitted from analysis because the quail eggs were not damaged, even though the plasticine eggs and nests appeared to have been eaten by rabbits (*Sylvilagus* sp.). We assumed that rabbits were not actual nest predators because they did not consume the quail eggs.

Nests on the 6 fragments were depredated at higher rates than nests on the 4 unfragmented sites (Figure 1; $U_1 = 5.00$, $U_2 = 19.00$, $P = 0.084$). With nests as the unit of replication, we find a similar result ($G = 6.81$, $P = 0.009$). Mean predation rates were also higher on fragments than unfragmented sites across all 4 microhabitats (Figure 2). These differences in predation were especially pronounced in the forb ($U_1 = 3.00$, $U_2 = 21.00$, $P = 0.033$) and rootball/stump ($U_1 = 2.50$, $U_2 = 21.50$, $P = 0.019$) microhabitats, though the same trends were present in the sapling/shrub ($U_1 = 8.00$, $U_2 = 16.00$, $P = 0.238$) and log ($U_1 = 7.50$, $U_2 = 16.50$, $P = 0.176$) microhabitats. The patterns were identical at the nest level (forb $G = 6.94$, $P = 0.008$; rootball/stump $G = 3.31$, $P = 0.068$; sapling/shrub $G = 0.0197$, $P = 0.657$; log $G = 1.45$, $P = 0.228$).

The differences in predation rates between fragments and unfragmented sites were reflected in differences in the predators recorded in each treatment. The absolute number of predation events identified as small and medium sized mammals was nearly identical

in fragments and unfragmented sites, but all identified large mammal and nearly all bird predation events occurred on fragments (Figure 3). In addition, a disproportionate number of nests moved by predators (25 of 29) and nests with unknown predators (18 of 23) were on fragment sites (Figure 3). These data suggest that the observed difference in predation rate between fragments and unfragmented sites is due to the presence of additional predators on the fragments that were absent or rare at unfragmented sites.

The edge class in which nests were placed on fragments was a significant predictor of nest predation in the logistic regression analysis ($P < 0.001$; Table 2). In contrast, nest microhabitat was not a significant predictor when included in the logistic regression with edge class. This suggests that the risk of nest predation may be better predicted by the distance of a nest from the forest edge, than by the specific microhabitat. Interestingly, the mean predation rate in fragment interiors > 30 m from the edge ($\bar{x}$ = 0.26, n = 43) was nearly equal to the mean predation rate for unfragmented sites ($\bar{x}$ = 0.24, n = 147), which implies that the effect of edge on nest predation may be limited to distances of 30 m.

Discussion

We found evidence of increased nest predation within historically fragmented forests in southwestern Oregon, which are currently embedded in a matrix of clearcuts. All trends in the data suggest fragmentation has negative effects on nesting success, as indexed by predation on artificial nests. Because our study area was fragmented by timber harvest (as opposed to urban or agricultural land), and because it historically was naturally fragmented, our results are unusual.

The elevated predation rate in forest fragments was consistent regardless of the analysis we used. Forest fragments experienced an overall higher rate of predation than continuous forest, consistently higher rates of predation across 4 nesting microhabitats, and elevated predation rates near edges. It appears that the differences in predation rate between fragment and unfragmented sites was largely driven by elevated predation within 30 m of fragment edges. Thus, it appears that forest fragment edges may be particularly problematic for nesting birds.

Although we can only speculate about which species were responsible for increased predation on fragments, we feel confident inferring that elevated predation was accompanied by a shift in predator size. Several lines of evidence suggest that increases on fragments were caused by predators that were generally larger than those found on controls. First, a disproportionate number of nests within fragments were moved during predation. Second, there were far more predation events on fragments than on controls for which no predator group could be assigned because evidence was removed. Third, although the sample sizes are small, it is notable that all predation events ascribed to large mammals (3 of 3) and almost all events ascribed to large birds (4 of 5) were on fragments. Interestingly, a study in the southeastern U.S. found patterns similar to ours: predation by small predators was about equal on small and large fragments, and elevated predation on small fragments was caused by large predators (Keyser et al. 1998).

The negative effects of fragmentation that we recorded are likely due to interactions of the landscape and predator community. Marzluff and Restani (1999) proposed that birds may suffer increased nest predation within timber-harvested landscapes when regenerating clearcuts support large populations of berry-producing

plants which in turn support generalist predators. Indeed, thimbleberry (*Rubus parviflorus*), trailing blackberry (*Rubus ursinus*), black raspberry (*Rubus leucodermis*), and currant (*Ribes* spp.) were common in many of the clearcuts surrounding our study sites.

Although the strength of our study is to detect relative differences and not to infer actual rates of predation for bird species, we feel that the differences in predation between microhabitats may have implications for the model species. Within our study area, the Pacific-slope flycatcher and the winter wren have been shown to prefer late successional forests, and both species commonly nest in what we labeled the rootball/stump microhabitat (Ehrlich et al. 1988, Ralph et al. 1991). This microhabitat suffered unusually high predation within fragments. If these species commonly attempt to nest within remaining fragments of old forest, and if predation rates are high within their preferred nesting microhabitats, the remnants may be serving as "ecological traps" (Gates and Gysel 1978).

Previous research in timber-harvested forests has generally not found negative effects of fragmentation on breeding birds (Andren 1995). Furthermore, the dominant paradigm in recent literature is that species in forests historically fragmented by natural processes may be resilient to current anthropogenic fragmentation. This idea is often stated in the context of the ecology of breeding birds in coniferous forests of western North America, where most studies have failed to find evidence of deleterious fragmentation effects on nesting birds (Schieck et al. 1995, Bayne and Hobson 1997, Schmiegelow et al. 1997, Tewksbury et al. 1998, Berry and Bock 1998, Sallabanks et al. 1999). Clearly our findings do not provide evidence in support of this paradigm.

Inferences about breeding productivity of birds made from artificial nest data are controversial, in large part due to differences from real nests (Martin 1987, Major and Kendal 1996, Haskell 1995). We used artificial nests because they allowed us to obtain adequate samples sizes and a controlled distribution of nests that would not have been possible with real nests. To help keep our inferences conservative, we focused on relative differences in predation between nests in different locations rather than absolute predation rates. Ultimately, studies of real bird nests will be necessary to confirm these results.

Our results point to several other useful avenues for future research. First, an examination of the relationship between predator communities and food plants in the habitat matrix would be useful. In addition, it would be useful to determine where timber harvest is likely to have the least and greatest impact on productivity of bird species by examining nest success in harvested forests that differ in natural historical disturbance frequency and forest age. Finally, comparisons of nesting success in western coniferous forests fragmented by timber harvest versus those fragmented by natural processes would be informative.

Management Implications

Because all biological trends in the data were consistent, and effects sizes were large, the management implications of our findings are important (Johnson 1999). Our results show that historically naturally fragmented forests now structured through timber harvest can be subject to the same type of negative fragmentation effects commonly found in forests surrounded by agriculture and human habitation. It is likely that the

negative effects of timber harvest on nest success are linked to the fact that naturally fragmented forests and those fragmented by timber harvest tend to differ in the scale of disturbances, amount of forest edge, the abundance and biomass of snags and coarse woody debris, and the diversity and biomass of young trees (Hansen et al. 1991). We speculate that the negative effects we recorded could be decreased if these disparities were reduced. Given current management practices, however, our data indicate that it would be wrong for land managers to conclude that timber harvest will not affect vital rates of birds in forests that are naturally fragmented or that are surrounded by a matrix of regenerating forest.

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Table 1. Trial dates, site characteristics, and artificial nest predation rates for 4 unfragmented and 6 fragment sites in southwest Oregon, 1998.

Trial Dates	*Site Name*	*Site Type*	*Size (ha)*	*Number of Nests*	*Predation Rate*
11 June - 25 June	P	Unfragmented	>250	27	25.9
	S	Fragment	1.3	18	77.8
	PC	Fragment	0.9	13	61.5
27 June - 11 July	YA	Unfragmented	>250	33	12.1
	YB	Fragment	1.3	16	50.0
	YC	Fragment	1.2	19	57.9
4 July - 18 July	G	Unfragmented	>250	63	34.9
	GB	Fragment	6.5	60	21.7
23 July - 6 August	JA	Unfragmented	>250	24	8.3
	FB	Fragment	2.0	22	9.1

Table 2. Results of a logistic regression predicting fate of artificial nests[a] in southwest Oregon in 1998, using predictor variables distance to edge[b] and nest microhabitat[c], which were added to the model with block entry.

Variable	*Coefficient*	*SE*	*P*
Constant	0.2741	0.4250	
Edge	-0.3693	0.1049	0.0004
Microhabitat	-0.0001	0.1179	0.9991

[a] 0 = not depredated and 1 = depredated (i.e., either egg was removed from the nest, the real egg was cracked, or the plasticine egg showed clear tooth, claw, or beak marks).

[b] 1 = < 15 m, 2 = 16-30 m, 3 = 31-45 m, and 4 = > 45 m. All nests in unfragmented sites coded as edge class 4.

[c] 1 = sapling/shrub (nest at the base of a tree < 2m tall), 2 = forb (nest hidden on the ground within a patch of herbaceous plants), 3 = log (nest under a fallen log >12cm dbh), and 4 = rootball/stump (nest in the rootball of a fallen tree or nest in the crevice of a stump left by a fallen snag).

Appendix A. Nest microhabitats used when placing artificial nests in timber managed forests in southwest Oregon, matched with location descriptions and associated model bird species[a].

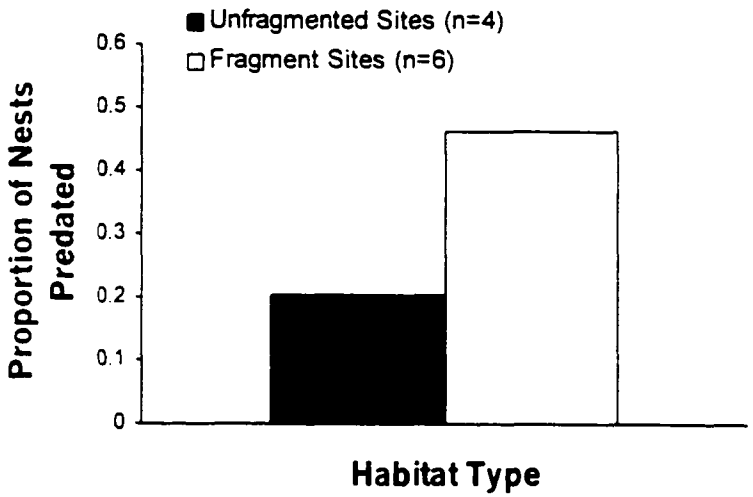
Nest Microhabitat	*Location Description*	*Associated Bird Species*
Forb	On the ground within a patch of herbaceous plants.	Dark-eyed junco
Rootball/Stump	In the crevice of a stump left by a fallen snag, or in the rootball of a fallen tree.	Pacific-slope flycatcher Townsend's solitaire Winter wren
Log	Under a fallen log >12cm dbh.	Dark-eyed junco Townsend's solitaire
Sapling/Shrub	At the base of a tree or shrub < 2m tall.	Dark-eyed junco

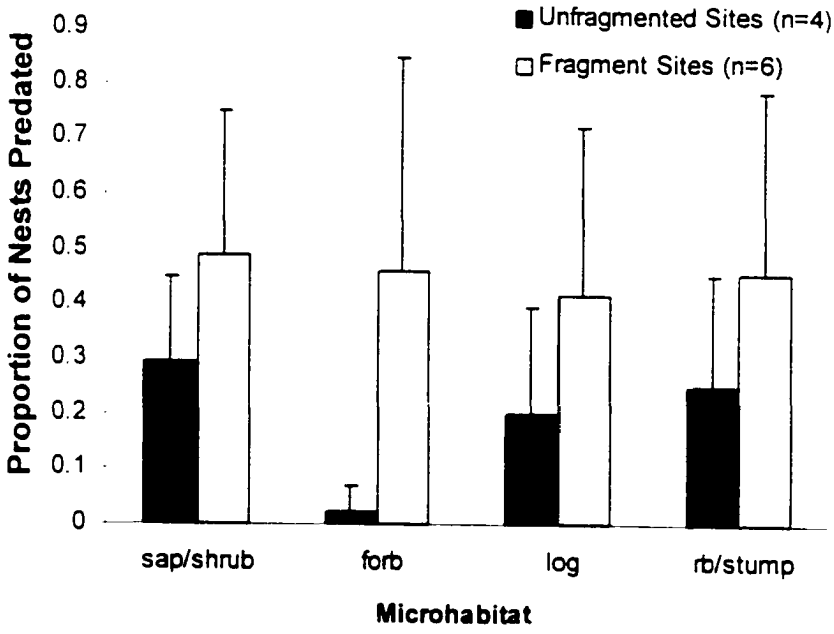
[a] Species known to nest in our study area within each of the microhabitats (K. Jones, personal observation; Ehrlich et al. 1988).

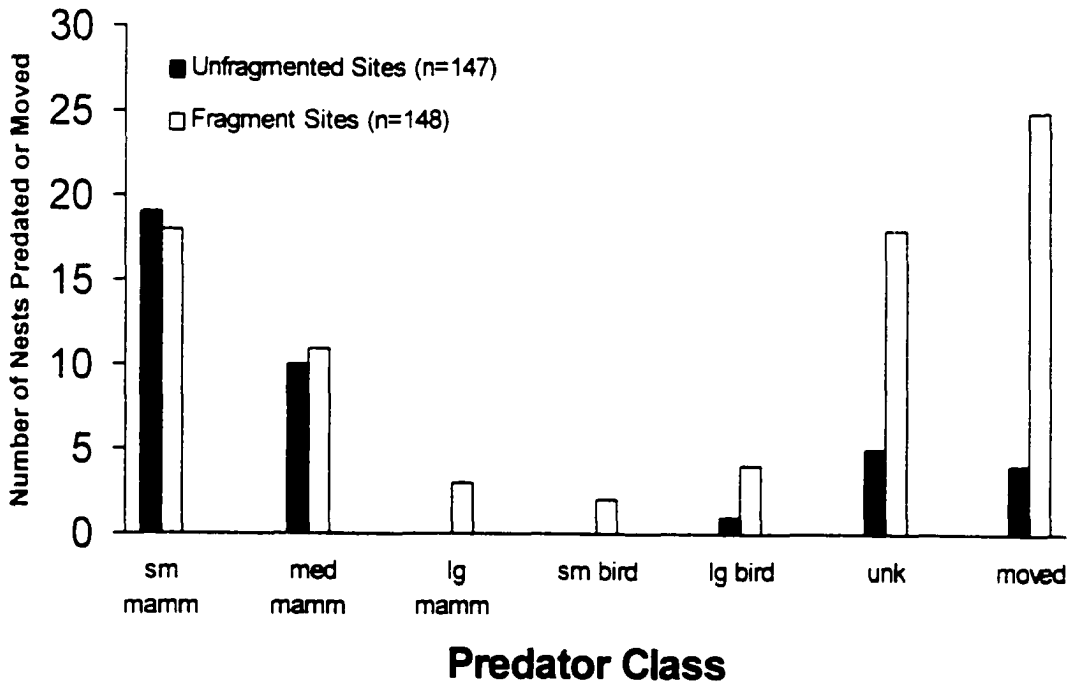
Figure 1. Mean proportion (+1 SE) of artificial nests depredated during a 14-day period on unfragmented (closed bar) and fragment (open bar) sites in southwest Oregon, 1998.

Figure 2. Mean proportion (+1 SE) of nests depredated for unfragmented (closed bars) and fragment (open bars) sites within each of four microhabitats: sapling/shrub, forb, log, and rootball/stump.

Figure 3. The number of nests depredated by each predator class on unfragmented (closed bars) and fragment (open bars) sites in southwest Oregon between 11 Jun and 6 Aug, 1998.







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